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GENE AND ORGANISM*

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The subject which I wish to discuss is the concept of organism, as it appears to a geneticist. I shall ultimately use a broad enough definition to include non-living as well as living systems under the term. Genes enter in as the keystone of the bridge connecting these.

PART I. THE HIERARCHY OF ORGANISMS

Webster's dictionary gives as its second definition of "organism" (the first being merely as a synonym of organic structure or organization) "an individual constituted to carry on the activities of life by means of parts or organs, more or less separate in function but mutually dependent; any living being; any animal or plant."

The phrase "activities of life" may be taken to include primarily all physiological processes and behavior tending toward persistence of the individual, but with "persistence" qualified of course by growth, development and adaptive change. Secondarily it includes the reproductive processes that tend toward persistence and multiplication of the type.

The mutual dependence of parts stressed in the definition is exhibited to widely varying extents among plants and animals. In some of the lower forms, there is little more than physical continuity among parts that carry on their activities almost independently. In some thallophytes and all higher plants, a closer integration is brought about by vascular bundles. Most animals are integrated not only by physical continuity and a common vascular system but by a nervous system: a loose nerve net in lower forms, a central nervous system in higher ones.

About a century and a half ago it began to be recognized that all but certain microscopic plants and animals are composed of somewhat similar microscopic bodies, cells, each of which carries on its life processes largely by and for itself. It gradually became clear that cells arise only by division of preexistent cells. The concept that cells are organisms in the strictest sense has been borne out by studies of tissue cultures. The familiar organisms are thus recognized to be also colonies of organisms.

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In many cases, the scope of the concept of a hierarchy of organisms is extended in the other direction by the occurrence of colonies of multicellular individuals that arise by processes of budding and incomplete separation. Again there may be little more than physical continuity as an integrating principle but in some cases there is such a division of labor among the zooids as to constitute the whole as a single well defined organism. In certain Bryozoan colonies integration reaches the level of instantaneous coordinate behavior through the development of a common nervous system. It is a plausible hypothesis that the individual annelid and ultimately the individual arthropod represent the integration of what was ancestrally a mere chain of zooids into a single much more complex organism.

Webster's dictionary goes on to a third, broader definition of organism "any thing, structure or totality of correlative parts, in which the relationship of part to part involves a relationship of part to whole, thus making it self-inclusive and self-dependent."

With some straining, this definition applies to any whole species of biparentally reproducing plant or animal, defined as a population in which there is effective continuity of interbreeding. Biparental reproduction is here the integrating principle which makes the species a single loosely knit organism, with characteristics that are more than those of a mere aggregation of similar individuals. These characteristics include not only averages of the characters of the individuals but also variability within and between subspecies and local populations or demes.

The species tends to maintain its characteristics through generation after generation of replacement of the individuals, but with both short-time and long-time adaptations to changes in the environment. There is an evolutionary history somewhat comparable to the ontogeny of individuals but differing in its much higher degree of uniqueness. The species may also divide but again in a much less repetitive way than individuals. The species differs notably from an individual organism in its lack of physical continuity at any given time, but even in this respect there is literal protoplasmic continuity in the form of a complex network in terms of space-time.

In many higher animals, biparental reproduction is supplemented by social instincts in the integration of local populations into entities which have organismic properties of a less abstract sort than those of species. Organization of this sort reaches its climax in the colonies of ants, bees and termites (cf. Wheeler, 1911; von Frisch, 1950; Emerson, 1939).

These modes of integration are further supplemented in man by the capacity for symbolic speech and the consequent evolution of culture, independent of physical evolution. It is just over 300 years since Hobbes developed the analogy between human society and a living organism. The topic has been discussed recently in terms of modern society by Gerard (1940).

The human social organism, while composed primarily of human beings, may also be considered to include peripherally domestic animals, cultivated

plants and indeed land, buildings and machinery, just as the individual plant or animal, or the individual cell may contain much relatively inert material. Animal colonies, for example, those of ants, may be similarly heterogeneous.

It is evident that the organismic concept does not necessarily imply a hierarchy. This is sufficiently familiar in the multifarious overlapping of social groups in human society. The social organisms of animals and man cut across the hierarchy of interbreeding groups.

This becomes even more conspicuous if we consider the entire array of plants and animals and peripherally the soil and waters of a given region as an interdependent self-regulatory system, with considerable persistence, qualified by a characteristic type of history (biotic succession) and hence an organism in the broad sense. Since regions are connected, the entire biota and peripherally the surface of the earth form one great organism.

Turning to the non-living world, LaPlace, a century and a half ago, directed his major efforts toward proving that the solar system is to a high degree a self-regulatory system. The term organism is applicable in its broadest sense to the sun and its planets and to the stars in general because of their high degrees of persistence qualified by their more or less orderly histories. The universe as a whole is the all inclusive organism.

At the opposite extreme in size, electrons and photons do not seem to come under even Webster's broad definition since they have no parts to be interdependent as far as known. The vibratory character of both, however, implies interdependent phases. Moreover, they share with organisms, the property of persistence, although to very different degrees.

The atom has interdependent parts and self-regulatory properties that clearly put it in the class of organism in this broad sense. The same is true of the molecule, higher in level in the hierarchy, but with less integration.

In an orderly system of molecules we find the reproductive capacity in an elementary form in the capacity of a crystal to grow according to its pattern, at the expense of unorganized material. The impossibility of initiating crystal growth in some cases without a seed crystal resembles the origin of cells only from preexistent cells.

There has, however, seemed until recently to be an unbridgeable gap in kind between the non-living molecule and the living cell. It is apparent now that this gap is being bridged to a considerable extent by such entities as bacterial transforming principles, genes and viruses. On the one hand, there is reason to believe that the essential patterns of these entities are of the same sort as that of a giant chemical molecule—desoxyribose nucleic-acid in the case of the free pneumococcus transforming principle, the same in association with protein in the case of the gene, and crystallizable nucleoprotein in the case of free tobacco mosaic virus. The free transforming principle and the free virus seem to have none of the properties of life, but within a living cell both of these entities as well as the gene share the property of a living, even though parasitic, organism of not

only maintaining the integrity of a very complex pattern, but also of duplicating this pattern, irrespective (within limits) of the surroundings.

Whether we consider the gene and allied entities as actually living depends on the weight given to autonomy in different respects. All of these entities apparently depend on the metabolic processes of living cells in their reproduction. Autonomy, however, is always a relative matter. Higher animals and man are far more highly integrated organisms than green plants, but are dependent on the latter with respect to energy-rich organic compounds. Genes, viruses and transforming principles are living if autonomy of pattern rather than metabolic independence is made the criterion. They are living according to Cuvier's famous definition (at least if atom or radical is substituted for molecule) (Osborn, 1917, p. 51). In translation, "Life is thus a vortex, more or less rapid, more or less complicated, of which the direction is constant and which always involves molecules of the same sorts but into which the individual molecules continually enter and from which they continually depart in such a way that the form of the living body is more essential to it than the matter."

The mode of organization of the genic material is a subject on which there is still room for considerable difference of opinion. In discussion of it, we must distinguish organization with respect to various properties which need not be perfectly correlated. These include (1) self-duplication, (2) physiological action, (3) crossing-over, (4) breakage and rearrangement, (5) gene mutation.

The idea that the genetic chromosome functions as a whole with respect either to self-duplication (beyond mechanical continuity) or to physiological action is at once ruled out by the high proportion of gross rearrangements that persist and that cause only trivial if any changes in character.

At the opposite extreme is the hypothesis that the genetic chromosome is essentially a single enormously long molecule (for example, a polynucleotide) in which self-duplication is a point by point determination by the parent chain of the order of different kinds of nucleotides in a daughter chain as it is assembled under certain intracellular conditions. On this view, crossing-over and chromosomal breakage might be expected to occur more or less equally often between any two nucleotides and the genes as structural units tend to be reduced to the single nucleotides. Small chromosome aberrations (short inversions, deficiencies or duplications) would be expected to bring about a great deal of false allelism—mutations that appear to be strictly allelic to two or more point mutations that are not allelic to each other.

The mere cytologic appearance of uncoiled chromosomes with their thousands of identifiable chromomeres, indicates that the above hypothesis is too simple. There is clearly organization of the chromosome into entities, probably a hierarchy of entities, of intermediate size. Even with respect to the self-duplicative property, it is not unlikely that there are groupings larger than the ultimate building stones that act as wholes. If this is true, an important consequence is that the separation of components

of such blocks by rearrangement after breakage would necessarily result in loss of the self-duplicative property. Such a situation is suggested by the frequency with which rearrangements have a lethal effect. Under this hypothesis crossing-over would not occur within the self-duplicative blocks if it is a concomitant of duplication as in Belling's (1933) theory but would not necessarily be excluded if it occurs at a different phase than duplication.

Whatever the degree of integration with respect to the self-duplicative property, there can be little doubt that physiological action depends on the pattern of the genic material over considerable lengths. There is, moreover, much experimental evidence that the blocks defined by physiological properties are also ones within which either crossing-over or separation into components that retain the self-duplicative property after breakage and rearrangement are very infrequent. A strong correlation between the units of self-duplication and of physiological action is to be expected if the primary gene products are formed by a process that is essentially the same as duplication.

The complexity of pattern within blocks characterized by a certain general type of physiological action is especially clearly indicated in the case of genes that are related to antigens. It seems to be the rule that single loci are concerned with many distinguishable antigenic properties (man (Wiener et al., 1947); (Race and Sanger, 1950), cattle (Stormont et al., 1951), fowls (Briles et al., 1950), ducks (McGibbon, 1945), etc.). The most complicated so far analyzed seems to be the B system in cattle with 80 alleles involving combinations of 21 antigenic properties. In this and the other cases, there is no approach to the randomness of combination expected if there were multiple loci capable of exchange by crossing over even at rates comparable to those of mutation in rarity. There is instead the appearance of a complex pattern in which variable elements may exhibit all grades of dependence up to complete dependence of one on one or more others (for example, dependence of K of cattle on two largely independent properties, B and G). There are also all grades of incompatability up to the complete incompatibility that has suggested allelism in a narrow sense.

Most systems of multiple alleles, when carefully studied, are found to involve pleiotropic effects which seem to be primary, as indicated by differences among the orders of effect on the different characters. The simplest interpretation is that the mutations occur at different points in a complex pattern rather than at a single one.

That the gene or its product tends to function as a whole, in spite of complexity of pattern, is indicated by the usual lack of complementarity of different recessive mutations with respect to any given type of effect (intermediate heterozygote). Exceptions occur, however, in both directions to indicate that the correlation between the structural and physiological units is not perfect. There are cases in Drosophila (Bridges and Brehme 1944) in which recessive mutations with identical or nearly identical effects and no crossing-over nevertheless reconstitute type. On the other hand, there is an increasing number of cases (reviewed by Lewis, 1950) in

TABLE 1

Level of Organization		Description		Dynamics			Genetic aspect
Primary	Secondary	Climax phase	Secular change and reproduction	Persistence	Secular change	Reproduction	
Biota	World	Bio-geography	Paleontology	Theory of biotic evolution			Genetics of behavior
	Local	Descriptive synecology		Dynamic synecology			
Society	*Traditional Society* Mankind Nation Special groups	Cultural Anthropology	History	Sociology	Philosophy of history	Cultural cleavage	
	Instinctive society	Descriptive autecology		Dynamic autecology			
Interbreeding population	Species group Species Subspecies Deme	Taxonomy	Phylogeny	Theory of evolution Statics	Transformation	Speciation	Population genetics
Individual	Colony Individual Organ	Anatomy	Descriptive embryology	Physiology of organs	Physiology of development	Physiology of reproduction	Developmental genetics
Cell	Tissue Cell Cell constituent	Histology Cytology	Differentiation	General Physiology	Physiology of differentiation	Physiology of cell division	Physiological genetics
Gene	Linkage system Gene	Cytogenetics Genic chemistry	Nature of mutation	Physiology of persistence	Physiology of mutation	Physiology of duplication	Theory of the gene

which similar mutations, which can be recombined by rare crossing-over, have effects that suggest allelism (Lewis' S-type position effects). There seems no compelling a priori reason for supposing that mutations within a single structural unit should never have complementary effects, or that physiological integration should not extend over two or more structural units, especially if the latter are historically duplicates. It is likely that it will become necessary to recognize supergenes—(replicates of similar genic material, bounded by unconformities due to chromosomal rearrangements, and capable of rare internal crossing-over and of separation into persistent components after rearrangement) as well as genes in the conventional sense.

The fluctuating effects of heterochromatin on the functioning of neighboring genes over a considerable extent of the chromosome (Lewis' V-type of position effect) seem to be of an essentially different nature and should be included among the general conditions for gene functioning in contrast with the effects of change within the structures of the gene or supergene.

It will be convenient to conclude this survey of organisms with a subdivision of the field of biology, based primarily on level of organization and secondarily on the somewhat similar problems that arise at each level. These include the enormous problems of description of the climax phases and of the historical development of these, the problems of the dynamics of persistence and of change, and finally, at the lower levels, of reproduction. An additional dimension might well be added to include the various aspects of pathology—changes beyond the adaptive capacity of the organism (*cf.*, Link, 1932).

While the entities at the various levels all have general properties that justify the use of a common term, organism, the integrating principles and the relations to components differ enormously in kind. All of the cells of a single individual, for example, trace to a single cell at the beginning of the individual's history. The relation of cells to genes is, of course, utterly different. The fact that reproduction of individuals typically involves a sampling of the genes of the parents and ultimately of the species means that the interpretation of phenomena at all levels up to and including the species must be based not only on the next lower level but also directly on the genes. A column in the table is thus reserved for the genetic aspect.

PART II. THE INNER NATURE OF ORGANISMS

The type of organism with which we are most intimately acquainted—that of human beings and especially ourselves—seems to differ so in kind from most of the things that I have referred to as organisms that the use of the single term to include them all may have seemed strained beyond the possibility of value. We are aware of a unified stream of consciousness in ourselves and attribute such a stream to other human beings. We may speak of the spirit of America or of mankind, but only figuratively. We find extreme difficulty in conceiving of a really unified stream of consciousness of a society. Still less, however, can we conceive of the consciousness of a DNA molecule.

In the ordinary affairs of life, there is no practical difficulty in thinking in terms of a world consisting largely of inert things, each pushed or pulled around by others and these by others, according to certain immutable laws of nature, but here and there (in man and perhaps the higher animals) inhabited by minds that perceive what is going on and somehow manage to do something about it. The physicist as well as the humanist can go along without much trouble with this common sense, dualistic viewpoint. The biologist is continually in trouble. He may decide, with Jacques Loeb, to interpret all biological as well as physical phenomena as wholly mechanistic and not run into difficulties in principle even in analyzing human behavior—no difficulties, that is, until he comes to himself. His own stream of consciousness, of which all his impressions of the outside world are a part, cannot be described adequately in terms of changing spatial relations among particles or of changing fields. He can maintain the integrity of his concept of nature only by treating minds as mere observers, without influence on the inexorable course of events.

Another biologist, starting from his own stream of consciousness and capacity for voluntary action, as his basic data, finds such similarity in the behavior of other human beings to his own, that he unhesitatingly ascribes consciousness and a similar power of voluntary action to them. In this he is far from alone, but essentially the same argument leads him to ascribe consciousness and choice to at least the higher vertebrates. He still has plenty of company, but on comparing the behavior of lower vertebrates and of invertebrates, including the protozoa, he finds no abrupt difference in kind. He tends to interpret the behavior of all of them anthropomorphically in terms of sensations, conscious integration of these, and conscious choices of action (no doubt losing more and more company as he goes down the scale). But if he ascribes mind to protozoa the absence of any discontinuity suggests that he must also ascribe it to protophyta and to the individual cells of animals and plants. He is led now to the conclusion that his own apparently unified stream of consciousness is somehow a fusion of the minds of the cells of which he is composed and he is back to the problem of the social mind, but here as the one thing of which he is directly aware, instead of as a mere figure of speech, unimaginable as a reality.

The argument from continuity may take a different course. Instead of studying behavior along the evolutionary sequence of organisms, the biologist may trace its development in the individual human being. Again he finds no definite point at which he can say that mind is present but not present earlier. He is carried back again to a single cell and back of this to two wholly separate cells. Aristotle settled the difficulty of the apparently dual origin of the unified personality by deriving the form determining principle (the entelechy) from one parent, the father, while supposing that the mother merely supplies matter on which this operates (cf. Nordenskiöld, 1928). Modern genetics finds no evidence of any such difference in kind. There is equal inheritance of behavioristic, as well

as of morphological traits, from both parents and both depend on an array of genes ultimately derived in a largely random fashion from the whole population. If we are not at some point to postulate the abrupt origin of mind, mind must be traced to the genes, which presumably means to nucleoprotein molecules.

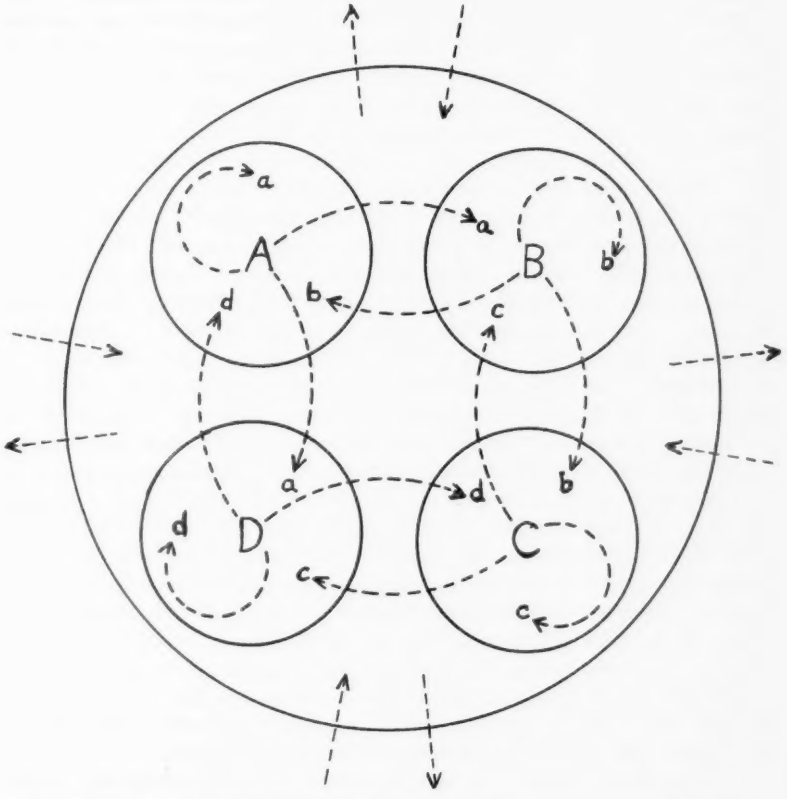

FIGURE 1. A, B, C and D represent partially isolated minds, each of which includes sensations (a, b, c, d) derived from its own actions and actions of others in the system, from which each interprets itself and others as matter organized in a certain pattern in a frame of reference (its space and time). The pattern of interactions of A, B, C and D constitutes a single mind at a higher level of organization and so on.

Lloyd Morgan compared the emergence of mind from matter in the course of evolution to the emergence of new organs. The emergence of mind in the course of individual development might similarly be compared to the emergence of the complex central nervous system from a simple neural tube and this from flat ectoderm. We may indeed accept the view that there is a development of the complex from the simple in mind, comparable to that

which takes place in structure, but the emergence of even the simplest mind from no mind at all seems to me at least utterly incomprehensible.

If, on the other hand, we turn the problem around and try to derive matter from mind, there is no such difficulty. We assume here that reality consists primarily of a multiplicity of minds—streams of consciousness—largely but not completely isolated from each other. The content of each consists of incursions of others, the working over of these into patterns that have value to it, and of choices of action based thereon. Each constructs (mentally) an "external" spatial world of matter from the regularities, not of its own choosing, of which it becomes aware in its stream of consciousness. Each center of consciousness thus has two aspects, as it is to itself—mind—and as it seems to others—interpreted as matter, but also primarily mental consisting as it does of aspects of these other minds. It is fortunate for simple minds that the relations among them can be interpreted by each in terms of only 4 dimensions: two dimensions of "direction" (the smallest number that permits immediate relations of each to many), one of "distance" (which permits the *absence* of immediate relation of each to many but the possibility of such relation at other times), and finally the order of succession of events, that is, "time" itself.

Needless to say this is not the commonest solution of the mind-body problem. I shall not attempt to go much into its history. As far as I am concerned, I may say that I derived it from a combination of Bergson's *Creative Evolution* (Translation, 1911), which impressed me greatly when I read it in 1912 but left me as completely mechanistic in my actual thinking as before, and Karl Pearson's *Grammar of Science* (1899), read in 1914, from which I emerged with the conviction that this is the only hypothesis that makes sense. I have referred to it a number of times, largely in connection with the theory of evolution (1921, 1931, 1935, 1941, 1948). Pearson's ideas trace to those of the mathematician Clifford (1879) who expresses the concept very clearly. More recently, Troland (1922) has developed the theory in its application to physics. He traces it through various authors to Fechner in 1863. A somewhat similar view has been elaborated into a philosophical system by Whitehead (1925).

The greatest difficulty as already noted is in conceiving of a single stream of consciousness as coming out of multiple separate ones, a real group mind from the fusion of the minds of individuals. About all that I can say is that the unity of my own stream of consciousness, such as it is, convinces me that such a coordination does occur and that the degree of physical integration exhibited by organisms is the external aspect of the degree of such internal coordination. It should be emphasized that the isolation of elements of mind can be only partial on this general view. They are not the windowless monads of Leibniz. They not only have effects on each other but if direct these must be of the nature of a common consciousness, however momentary, with momentary interaction. In tightly knit organisms such as animals with a central nervous system there is such an incessant interaction among the parts as to indicate a high degree

of integration of mind. A polymeric molecule, a multicellular plant, a sponge and a society even of ants, termites or men, is very loosely knit as compared with these. The organization of a species is merely that of a network and it would seem that common consciousness can only be similarly organized, that is, restricted to the consciousness of kind in encounters between members of the same species of higher animal and, of course, very much more elementary than this in the cross pollination of plants. Similar considerations apply to the biota of regions or of the world. The material universe on this view is the external aspect of the single all-inclusive world of mind postulated by the theory. As an organism, however, it seems so loosely knit that if we define an instant as the period of time required for communication and action between parts, an instant may be of the order of millions of years for the universe in comparison with a few hundredths of a second within the human central nervous system. But this very difference in scale may make it as impossible for the human mind to grasp the unity of the whole as it would be for a hydrogen atom to grasp that of the human organism. For a penetrating discussion of the universe as the all-inclusive organism compare Hartshorne, 1942.

Other difficulties with the dual aspect concept are the enormous repetitiousness and apparent lack of spontaneity of most things. With respect to the former it must be admitted at once that there appear to be severe limits on the kinds of pattern that are capable of organismic properties, especially at the lower levels. With respect to lack of spontaneity the movements of non-living things seem to be completely determined by immutable laws of nature. As Pearson pointed out, however, these laws of nature are merely condensed descriptions of how things are observed to behave. It has long been recognized that the gas law, $PV = RT$, is merely a statistical law, the resultant of such net regularity as there is in the behavior of an enormous number of molecules each of which is following a unique course. There is no necessary difference between the linear relation of volume to temperature in an enclosed gas at constant pressure and, for example, that of the fluctuations of the marriage rate in England and Wales to the fluctuations in foreign trade (correlation +.86 in the period 1861-1895, Hooker in Yule and Kendall, 1937, p. 296), although in the latter the course of action of the entities is based on choice.

The force of this objection to the universality of mind has greatly diminished since Pearson wrote the *Grammar of Science*. With the development of quantum mechanics and its indeterminacy principle, it appears that all of the ultimate laws of physics are merely statistical in character. All predictions are merely statements of probabilities. The apparent high degree of determinacy in the behavior of most non-living things rests on the fact that most of these, considered as organisms, are extremely loosely knit aggregates of enormous numbers of entities. All but the regularities in behavior cancel out for all practical purposes in the merely statistical behavior of the whole.

For apparent spontaneity, we must turn to tightly knit organisms rather than to mere aggregations. An organism, for example a human being, contains an enormous number of physical particles but these are organized in such a way that a difference in behavior in a minute portion can lead to large scale differences in that of the whole in spite of completely regular behavior in all other parts. An organism is by its very nature a system of trigger mechanisms which precludes merely statistical behavior. It is not, however, that the behavior of the whole is easily subject to indeterminacies of behavior at the quantum level. There are self-regulatory processes that usually prevent this. It is rather that the organism can act as a whole without deviation in the customary behavior of the parts of more than infinitesimal amounts.

It is a rather remarkable phenomenon from the purely physical standpoint when many tons of metal rise from the ground in Newfoundland, move through the air over the Atlantic Ocean and finally settle down gently at Shannon Field in Ireland. Yet an engineer studying the air pressure in the wings and ailerons of the plane in question, the movements of the ailerons and their relation to certain lever movements, the motion of the propellors, the mechanical relations to the motor and the gas explosions in the latter would find that the plane was merely following a necessary course, determined at all moments by well established physical principles, except that he would not understand on this basis the succession of movements of the lever. This, however, would involve only an infinitesimal portion of the total energy transactions. A physiologist, taking up the interpretation here, would find that the levers moved as they did because of a certain succession of muscle contractions and that these were in full accord with the principle of conservation of energy. He might trace the energy transformations in great detail around the adenosin triphosphate cycle, the creatine cycle, the phosphorylation and dephosphorylation of glucose in its breakdown to pyruvic acid, the 4-carbon cycle, etc. All energy transactions might be accounted for except perhaps infinitesimal portions of the total, involved in determining which muscles contracted. Another physiologist might then take over and trace what happened in the neuromuscular junctions and in the nerves. The energy transactions here are only an infinitesimal portion of an infinitesimal but he would find that the conservation law still applied except perhaps for infinitesimals of the third order in events at synapses in the nervous system. The flight of the plane would all be accounted for mechanistically except for something like an infinite regress of infinitesimals. Yet the whole was according to plan.

We have been led to the concept that the essential nature of all reality is that of mind. The active aspect of mind as we perceive it in ourselves is a creative process, will or choice based on values. The logical conclusion is that the course of events is governed by choice, not sporadically here and there but completely. There are, however, an enormous number of largely separate minds and what happens anywhere at any time is not

the choice of any one participant but a resolution of the choices of all, at all levels of organization from the lowest to the highest.

Choice is not caprice. With persistence in the face of difficulties at its core, it leads to behavior in which regularity may often be much more apparent externally than novelty. The processes of nature on this view are of a sort in which the internal creative unity of each event may be given the most convenient external representation by resolution into two ideal components, a purely deterministic one, and a deviation that appears random in character in a statistical study of more or less similar events. Statistical study leads to means and standard deviations. Even the latter, however, describe merely second order statistical regularities from which the unique creative aspect of each individual event still escapes.

It is the task of science, as a collective human undertaking, to describe from the *external* side, (on which alone agreement is possible), such statistical regularity as there is in a world in which every event has a unique aspect, and to indicate where possible the limits of such description. It is not part of its task to make imaginative interpretations of the internal aspect of reality—what it is like, for example, to be a lion, an ant or an ant hill, a liver cell, or a hydrogen ion. The only qualification is in the field of introspective psychology in which each human being is both observer and observed, and regularities may be established by comparing notes.

Science is thus a limited venture. It must act as if all phenomena were deterministic at least in the sense of determinable probabilities. It cannot properly explain the behavior of an amoeba as due partly to surface and other physical forces and partly to what the amoeba wants to do, without danger of something like 100 per cent duplication. It must stick to the former. It cannot introduce such principles as creative activity into its interpretation of evolution for similar reasons. The point of view indicated by a consideration of the hierarchy of physical and biological organisms, now being bridged by the concept of the gene, is one in which science deliberately accepts a rigorous limitation of its activities to the description of the external aspect of events. In carrying out this program, the scientist should not, however, deceive himself or others into thinking that he is giving an account of all of reality. The unique inner creative aspect of every event necessarily escapes him.

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THE BEHAVIOR OF AN X-RAY-INDUCED RING CHROMOSOME IN MAIZE[1]

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One of the most interesting problems in the field of cytogenetics involves the genetic and cytological study of ring-shaped chromosomes. They are invaluable as tools in cytogenetic studies, thanks to McClintock's (1938, 1941) thorough analysis of their behavior. Ring chromosomes are unstable. Owing to the formation of dicentric, double-sized rings followed by anaphase breakage, modified rings can result which are either deficient or duplicated for the chromatin present on the original ring. In a suitable genetic background, that is, when the homologous rod chromosomes carry the recessive allele and the ring carries the dominant gene, this ring chromosome behavior is manifested as a mosaic phenotype. Such mosaic plants yield only mosaic or recessive offspring upon self-pollination or backcrossing to the recessive. In the course of investigations involving X-ray-induced chromosomal aberrations in maize, two rings which showed aberrant behavior were found. Their behavior was abnormal in that, upon self-pollination, ring-carrying mosaic plants yielded offspring showing the full dominant phenotype as well as the expected mosaic and recessive types. This paper deals with the behavior of one of these rings.

Plants heterozygous for a luteus gene (l_{10}) on chromosome 6 were fertilized by X-rayed pollen from normal green plants homozygous for the dominant allele. The dosage used was 2000 r. Seeds from these plants were planted in the greenhouse. A number of striped plants mosaic for green and luteus tissue were found and later transplanted to the field for further study. One of these plants carried the ring chromosome to be described. The presence of the ring was first established cytologically

TABLE 1

F_2 DATA SHOWING CLOSE LINKAGE OF y_1 AND l_{10} $\left(\frac{Y_1\ L_{10}}{y_1\ l_{10}}\right)$

Plant No.	Yellow endosperm Green seedling	Yellow endosperm Luteus seedling	White endosperm Green seedling	White endosperm Luteus seedling
1832–3	185	1	1	56
1832–7	182	2	3	44
1833–1	263	1	1	88
1833–8	213	1	1	56
1834–9	364	3	1	113
Total	1207	8	7	357

[1]Work performed under Contract No. W-7405-eng-26 for the Atomic Energy Commission.

in meristematic cells of the root. The l_{10} gene is closely linked with y_1. Analysis of F_2 data showed 1 per cent crossing over between these two genes (table 1).

CYTOLOGICAL OBSERVATIONS

Upon self-pollination, the original striped plant segregated 20 green, 25 striped, and 71 luteus offspring. Further selfing of the F_1 striped plants yielded these three classes in approximately the same ratio. Pollen mother cells from a number of striped plants were examined and found to contain 19 rod chromosomes plus a ring. The ring is very large and involves chromosome 6, the nucleolar organizer chromosome. Pachytene configurations reveal that the ring and its homologous rod chromosome pair throughout most of their length (figs. 5, 6). Since the nucleolar organizer is in-

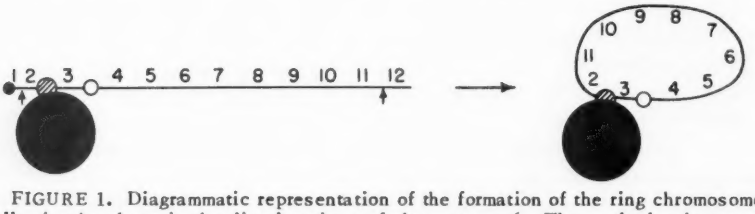


FIGURE 1. Diagrammatic representation of the formation of the ring chromosome following breakage in the distal regions of chromosome 6. The nucleolus is represented by the large black circle, and the centromere by the clear oval. The shaded area represents the nucleolar organizer. The arrows indicate the probable sites of X-ray-induced breakage.

cluded in the ring, one of the breaks must have occurred in the satellite region of the chromosome. None of the striped plants examined were trisomic for chromosome 6. It follows therefore, that gametes possessing 9 rod chromosomes plus the ring are viable. This leads to the obvious conclusion that the ring is deficient for only a small portion of the normal chromosome, and establishes the position of the second break as being in the very distal region of the long arm (fig. 1).

Meiotic anaphase configurations (P.M.C.) have a very high frequency of bridges—72 per cent. They are found in both first and second anaphases. They are not associated with acentric fragments and result from crossing over between the ring and its homologous rod. The anaphase configurations arising from the various types of single and double crossovers are shown in figure 2. Crossing over in the short arm of chromosome 6 between the centromere and the organizer is infrequent (McClintock, 1941), hence only crossovers in the long arm are considered. A single and a three-strand double exchange in which a ring chromatid is involved in both chiasmata (I) results in a single bridge in anaphase I only. A two-strand double exchange gives normal disjunction without a bridge. The second type of three-strand double in which a rod chromatid is involved in the two exchanges (II) results in a single bridge in both anaphase I and anaphase II.

A four-strand double exchange gives a double bridge in anaphase I. All these anaphase configurations have been observed (figs. 7, 8, 9). Dicentric double-sized rings also occur (fig. 10) and will be discussed in a subsequent paper.

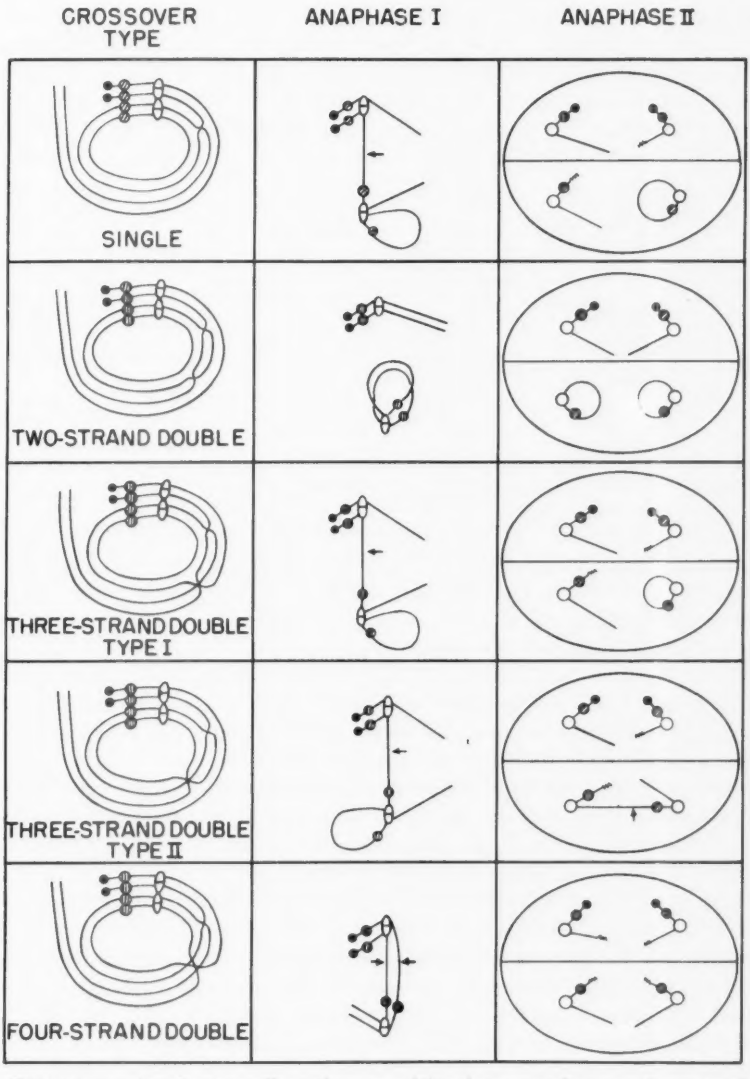


FIGURE 2. Anaphase configurations resulting from crossing over between the ring and its homologous rod chromosome.
—— broken chromosome end
——→ position of breakage of bridge

As is evident from figure 2, the anaphase bridge involves an entire chromosome 6 except the distal regions for which the ring is deficient. It is composed of part of a ring and part of a rod, the amount contributed by each being determined by the position of crossing over. The closer the exchange is to the centromere, the greater becomes the proportion of ring chromatin to rod chromatin involved in the bridge.

Ring-rod-ring cycle. Crossing over between the ring and its rod homologue accounts for the occurrence of green offspring in the progeny of self-pollinated striped plants. The green seedlings can arise in two ways. In the striped plants the dominant L_{10} gene is located on the ring and the re-

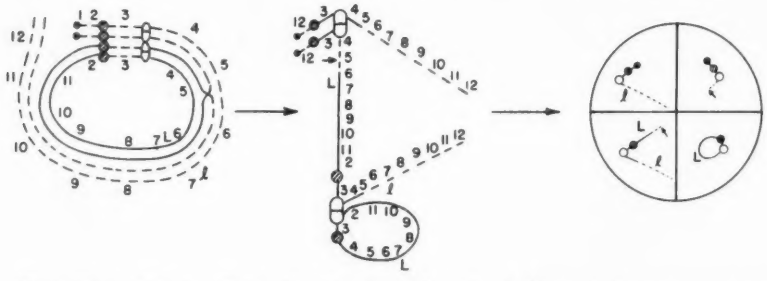


FIGURE 3. Diagram illustrating the formation of a duplicated chromosome carrying both the dominant and recessive luteus genes.

cessive allele on the rod. A two-strand and a three-strand double exchange of type II (ring chromatid involved in both chiasmata) where the chiasmata occur on both sides of the luteus locus will result in a double crossover rod chromatid carrying the *L* gene. Upon fertilization, a gamete possessing such a chromosome will give rise to a green plant.

Green progeny can also result from the conversion of a ring to a rod chromosome. This can be illustrated best by following the consequence of a single crossover between the ring and its homologous rod (figure 3). Such a crossover results in a noncrossover rod, a noncrossover ring, and a dicentric forming a single bridge in anaphase I. Breakage of the bridge at telophase gives rise to two rod chromosomes. Thus, whereas two rod and two ring chromatids are present at the onset of meiosis, there are three rods and one ring at its completion. One of the rings is converted into a rod. In the case of a four-strand double exchange, both rings are converted into rod chromosomes. Unless the bridge breaks in the region between 2 and 11, the site of the X-ray breakage which resulted in the formation of the ring, a deficient rod and a duplicated rod will result (that is, for those loci present in the ring chromosome). Let us assume that the l_{10} locus is at position 7. When a crossover occurs between this locus and the centromere the anaphase bridge will carry the dominant allele. Breakage of the bridge at position 4, 5, or 6 will give rise to a rod chromosome deficient for the l_{10} locus and a duplicated rod which carries the recessive gene in

its normal position and the dominant gene on the duplicated segment. Fertilization involving a gamete possessing such a duplicated chromosome will result in a green plant. In the endosperm such a chromosome will initiate the breakage-fusion-bridge cycle; however, in the embryo, the broken end will heal and the chromosome will persist unmodified (McClintock, 1941). Such a scheme is possible only on the male side, since the products of a single anaphase I bridge are not included in the egg nucleus. A double bridge is required for the inclusion of such a duplicated chromosome in the egg.

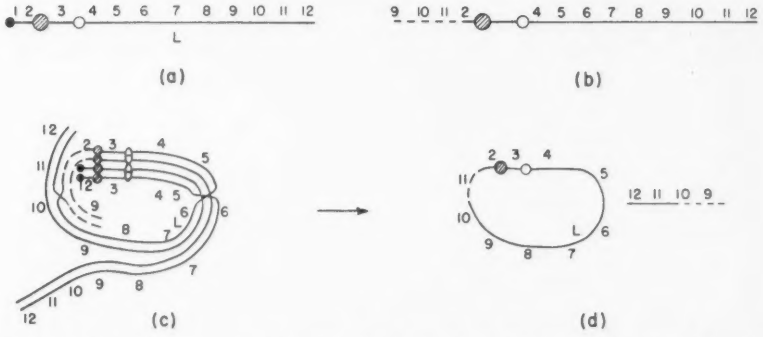
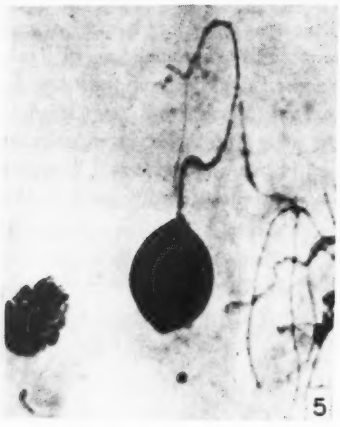


FIGURE 4. Diagrammatic illustration of the rod to ring conversion involving the duplicated chromosome of plant 1386-13. The normal chromosome 6 is shown in a; the duplicated chromosome is shown in b. The duplicated sector is indicated by a broken line. The type of meiotic pairing and crossing over required to give rise to a ring chromosome carrying the *L* gene is shown in c; d represents the recovered ring and acentric fragment. The fragment includes the entire duplicated sector.

The cytological distance between the l_{10} locus and the centromere is not known. The w_5 (or w_6) locus is the most proximal gene in the long arm of chromosome 6 (Demerec, 1923). The y_1 locus is 25 crossover units distal to this gene. Since l_{10} is closely linked with y_1 it must be at least 24 crossover units removed from the centromere and probably much more.

A green plant arising by the first mechanism described, possessing two normal chromosomes, would be expected to segregate green and luteus seedlings in a 3:1 ratio upon selfing. Green plants arising by the second mechanism, possessing a duplicated chromosome carrying both the dominant and recessive genes and a normal chromosome carrying the recessive allele, should segregate green and luteus seedlings in less than a 3:1 ratio because of reduced transmission of the unbalanced gametes through the male. Both these types have been observed. Fifteen F_1 green plants were self-pollinated. Thirteen plants showed a 3:1 segregation and one plant yielded a 2:1 segregation for green and luteus seedlings. The latter ratio would be obtained if the duplicated chromosome gave 100 per cent transmission through the egg and only 45 per cent transmission through the pollen.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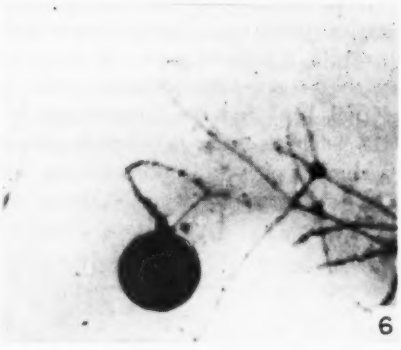
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7

8

9

10

The remaining green plant (1836–13) segregated striped as well as green and luteus offspring (40 green: 9 luteus: 6 striped). This is especially interesting since it represents a reconversion of the rod back to a ring, thus completing the ring-rod-ring cycle. This transformation occurs at meiosis as a consequence of pairing and crossing over involving the duplicated segment of the chromosome. The conversion of a ring to a rod and of a rod to a ring by crossing over has previously been reported in Drosophila (Morgan, 1933; Sidorov, Sokolov, and Trofimov, 1935, 1936; Sturtevant and Beadle, 1936; Novitski, 1951). The size of the recovered ring is independent of the length of the duplication and is equal to the size of the initial ring in the cycle. Cytological observation confirmed the presence of a ring chromosome in these striped plants. Four green sibs were studied and three were found to possess two normal chromosomes, while the fourth was heterozygous for a normal and a duplicated chromosome. The duplicated region in this plant was approximately one-fourth as long as the normal chromosome. Pachytene configurations showing pairing of the duplicated sector with its homologous segment in the long arm of the chromosome have been observed.

If the dominant gene were located on the duplicated chromosome, plant 1836–13 when selfed should have segregated green and luteus offspring in less than a 3: 1 ratio due to the reduced transmission of the duplicated gametes and the fact that some of the duplicated chromosomes were converted into rings. The excess of green plants indicates that the dominant gene was carried by the normal chromosome. The probable constitution of plant 1836–13 and the mechanism of rod to ring conversion are diagrammatically illustrated in figure 4.

NUCLEOLAR ORGANIZER. The inclusion of the nucleolar organizer region in the anaphase bridge results in a high frequency of aberrant spore quartets following meiosis. The aberrations involved the organization of the nucleolus. Normally, each cell of the quartet has one organizer and hence one nucleolus. The striped plants contained 32 per cent abnormal quartets which fell into eight different types. The aberrant types are shown in figure 4 and figures 11–18 and their relative frequencies of occurrence given in table 2.

McClintock (1934) has presented evidence to the effect that the mere presence of the nucleolar organizer in a cell is not sufficient for the organization of the nucleolus. The presence of a sizable deficiency in chromosome 6 inactivates the organizer, resulting in a diffuse or unorganized nucleolus. This has been corroborated by this study. All the abnormal types found are explicable on the bases that (1) the presence of

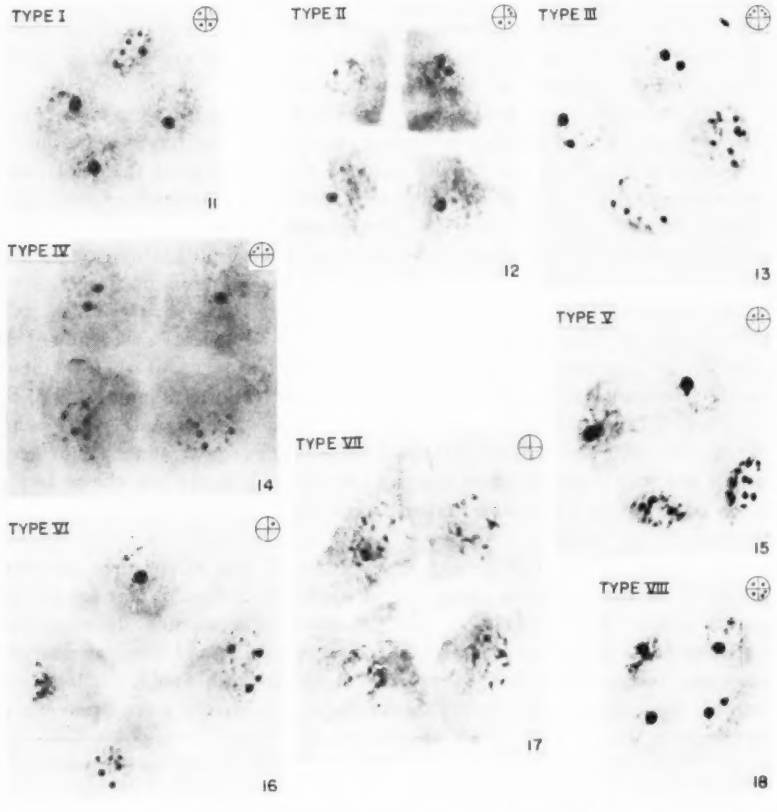
FIGURES 5 and 6. Pachytene. Synaptic association of a normal chromosome 6 with the ring.
FIGURE 7. Anaphase I. Single bridge.
FIGURE 8. Telophase I. Double bridge.
FIGURE 9. Anaphase II. Single bridge.
FIGURE 10. Telophase II. Double bridge (dicentric ring).

TABLE 2

FREQUENCIES OF QUARTET TYPES FOLLOWING MEIOSIS IN RING-BEARING STRIPED PLANTS

	Normal	Abnormal types							
		I	II	III	IV	V	VI	VII	VIII
Number	744	176	39	16	20	74	4	2	19
Per cent.	68	16.1	3.6	1.5	1.8	6.8	0.4	0.2	1.7

two organizers in a single cell can result in two nucleoli, (2) fusion can occur between two nucleoli in one cell, (3) the absence of the organizer or a large deficiency in chromosome 6 results in a diffuse nucleolus, and (4) a break in the organizer region gives rise to two functional organizers (type 8).



FIGURES 11–18. Abnormal spore quartet types arising in plants heterozygous for a ring and a normal chromosome 6.

Most of the abnormal spore quartet types can arise in a number of ways. Only one of the possible mechanisms responsible for each type will be presented. Region I refers to the long segment of the bridge between the nucleolus organizer and one of the centromeres; region II refers to the short segment between the organizer and the other centromere.

Type 1. Breakage of a single anaphase bridge in region I close to the centromere resulting in a deficient chromosome which inactivates the organizer

Type 2. Breakage of a single anaphase bridge in region II resulting in a duplicated chromosome carrying two organizers

Type 3. Breakage of each strand of a double AI bridge in region II resulting in two duplicated chromosomes, each carrying two organizers

Type 4. Same as type 3 followed by fusion of two nucleoli in one cell

Type 5. Breakage of each strand of a double AI bridge in region I close to the centromere resulting in two deficient chromosomes

Type 6. Breakage of an anaphase configuration resulting from a three-strand double crossover in which a rod chromatid is involved in both exchanges. This configuration gives a bridge in anaphase I and anaphase II. The anaphase I bridge breaks in region I close to the centromere resulting in a deficient chromosome. The anaphase II bridge does not break, remains on the spindle, and is not included in either telophase nucleus. Thus three of the four cells in the quartet have diffuse nucleoli; two because of the absence of the organizer and one resulting from the inactivation of the organizer by a large deficiency in chromosome 6

Type 7. Nonbreakage of a double AI bridge resulting in the exclusion of all four organizers from the telophase nuclei

Type 8. Breakage of a single anaphase bridge in the organizer region resulting in five functional organizers. The nucleoli in the binucleolated cell are of unequal size as has also been reported by McClintock (1934)

Since there are a number of ways by which the various abnormal quartet types can arise, it is not possible to make any generalizations about the breakage of the anaphase bridges. However, one thing is clear. The nucleolar organizer region is a weak spot on the chromatin bridge since it shows more breakage than would be expected considering its size in relation to the rest of the bridge. The frequency of quartets with five nucleoli is probably higher than the observed value since fusion of the nucleoli in the binucleolated cell would result in a normal-appearing quartet.

SUMMARY

The behavior of an X-ray-induced ring chromosome in maize involving almost the whole of chromosome 6 is described. By crossing over in ring-rod heterozygotes and breakage of the resultant anaphase bridges, the ring is frequently converted into a rod chromosome. Some of the rods carry a duplication and are transformed back to rings in subsequent meiotic divisions. The inclusion of the nucleolar organizer in the anaphase bridge results in a high frequency of aberrant spore quartet types.

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THE USE OF RADIOCOBALT AS A SOURCE OF GAMMA RAYS AND SOME EFFECTS OF CHRONIC IRRADIATION ON GROWING PLANTS

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INTRODUCTION

Many studies have been made on the effects of ionizing radiations on plants since Stadler's (1928) early use of X-rays and radium for inducing mutations about a quarter of a century ago. Until recently radium, X-ray machines or cyclotrons have been the main source of radiation. In recent years nuclear reactors, betatrons, etc., have been used as well as a variety of radioisotopes (Spinks et al., 1948; Conger and Giles, 1950; Sparrow and Christensen, 1950). Living material has been subjected to intense radiation from the explosions of the atomic bombs at Bikini and elsewhere (Randolph et al., 1948 and others).

In most cases the plants or seeds have been exposed to intense (acute) radiation for a comparatively short period of time (see reviews of Johnson, 1936; Catcheside, 1948). Stadler (1930) and Nebel (1941) both used a portable X-ray machine for irradiating flower buds of orchard trees, but it has not been practical until recently to expose growing plants for a prolonged period.

With the advent of the atomic energy program radioisotopes became abundant and fairly inexpensive, making it possible to obtain long half-life isotopes in sufficient quantity to permit irradiation of plants during their entire life span at reasonably high dose rates. This would have been possible before by using radium as a continuous gamma emitter, but the scarcity and high price of radium made this source impractical, except where the area or volume to be irradiated was very small or the dose rates used extremely low (see Gager, 1936).

Installation and Operation of Co^{60} Source. Cobalt^{60} was chosen as the most suitable of the radioisotopes for continuous gamma irradiation of plants under field conditions. It is fairly cheap to produce, and emits rather high energy gamma rays of 1.1 and 1.3 Mev. There is also a beta particle of .3 Mev but this radiation did not effect our experiments since the beta particles were absorbed by the stainless steel pipe housing the source. The half-life of Co^{60} is 5.3 years resulting in relatively small change in strength of the source during a growing season of 3–5 months.

The Co^{60} source was installed in a field and plants were grown in concentric circles (or arcs) around it (figs. 1 and 3). Since all points on a

*Research carried out at Brookhaven National Laboratory under the auspices of the U. S. Atomic Energy Commission.

given circle receive identical amounts of radiation a number of plants can be grown at any given dose rate. It is also possible to get a wide range of dose rates within a comparatively small area since radiation intensity decreases according to the inverse square law (table 1).

Because the source used emitted enough radiation to be a potential health hazard, it was necessary to arrange it in such a manner that the operators could move it into a suitable lead shield before approaching the area. This was achieved by installing the source in an upright metal tube

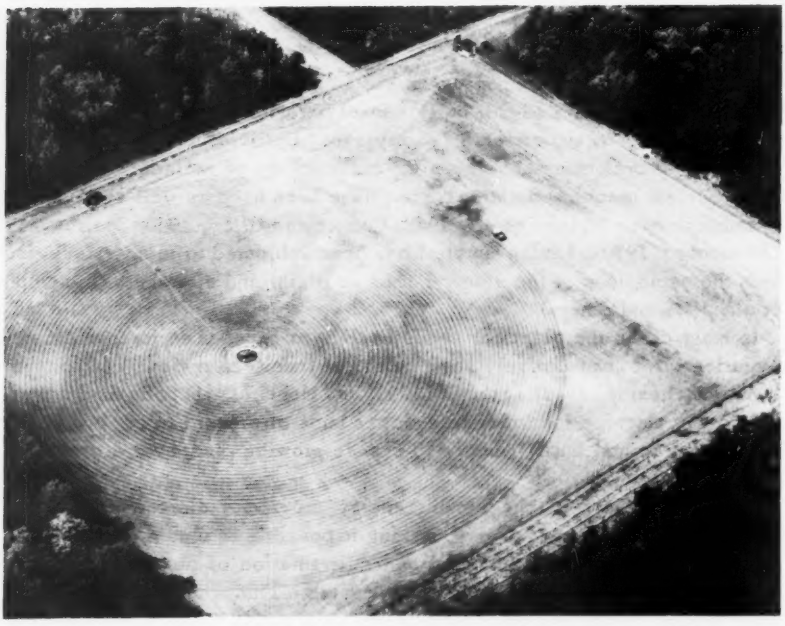

FIGURE 1. Aerial view of field marked ready for planting. Control house near upper right. Location of 145 curie source just left of center.

mounted on a cylindrical lead shield or "pig." The source could be elevated to the desired height during irradiation periods or lowered at other times by an underground cable attached to a windlass at least 70 meters from the source (140 meters with the 145 curie source; see fig. 2). The source was kept up (unshielded) as much as possible and was lowered (shielded) only when necessary for planting, cultivating, taking notes, collecting material, etc. Actually the source was in operation about 90 per cent of the time. An accurate log of the operations was kept so that it was possible to calculate exposure times and hence dosages whenever desired.

In a study of this kind the size of the source required (i.e. number of curies) depends in part on the amount of material to be irradiated, in part on type of effects to be studied (cytological, genetic or physiological), and in part on the severity of effect desired. The first two years (1949 and 1950)

a source of approximately 16 curies was used. This source emitted about 500 r per day measured at 1 meter, but only a few plants could be grown this close to the source and these required special handling. The nearest plants growing at soil level were 2 meters from the source (122 r/d, see table 1) and there was room for only a few at this position. Consequently, it seemed desirable to obtain a larger source and a 145 curie source was put into operation in 1951. With this source (approx. 1570 r/day at 2M, see table 1) the 7 meter circle received 113 r/d (comparable to the dose rate in the 2 M circle in the 16 curie field) and the 7 meter circle provided 3.5 times as much planting space. Thus by increasing the size of the source it was possible to have higher dose rates as well as more plants at any given intensity (see table 1 for comparative dose rates).

TABLE 1

APPROXIMATE DOSES IN ROENTGENS PER DAY AT VARIOUS DISTANCES FROM 16 AND 145 CURIES OF Co^{60}

Distance (meters)	1949 source (ca 16 curies) r/day	1951 source (ca 145 curies) r/day
1.5	218	2780
2	122	1570
3	53.6	670
4	30.4	368
5	19.0	230
6	13.1	156
7	9.6	113
8	7.5	86.2
10	4.7	54.2
12	3.3	37.2
14	2.4	27.0
16	1.8	20.4
20	1.1	12.7
24	0.73	8.6
28	0.52	6.2
32	0.41	4.7
40	0.24	2.9
50	0.15	1.8
64	0.084	1.05
75	....	0.73
100	....	0.39
140	....	0.12

With the 145 curie source in operation in 1951 physiological effects were apparent that were not observed in the 16 curie field. This is attributed to the fact that much higher dosages are required to produce serious physiological damage than to induce detectable numbers of gene or chromosomal changes. In choosing the size of the source it is desirable to have at least a small area in the field in which dosages are expected to be lethal or near lethal for the plants to be used. Rows farther from the source are of course used for cytological and genetic or morphological studies where larger numbers of plants are desirable.

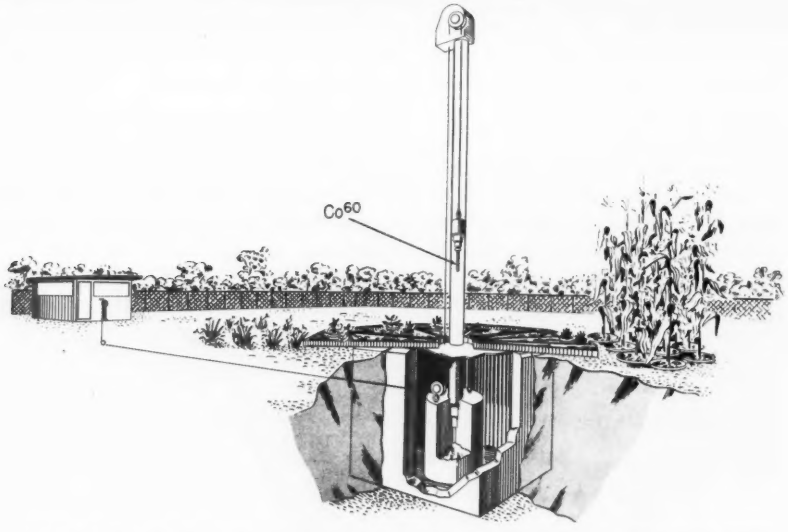

FIGURE 2. Diagram of installation showing underground remote control cable, lead pig, cobalt^{60} source and metal pipe housing the source.

The area immediately surrounding the steel pipe housing the source was covered by a set of twelve waterproofed wooden trays filled to a depth of an inch or so with coarse gravel. They were interconnected by pipes and a float valve in one regulated the water level so that the bottoms of the trays were always covered by water. The trays were used for pots and flats of germinating seeds or seedlings for high dosage exposures. These trays originally extended about 2 meters from the center but were reduced to 1 meter in 1952. The field was divided into 12 sectors, of which six alternate segments were used for genetic studies. The rest were used for the study of cytological and morphological changes.

In order to facilitate exposure of seeds at high dose rates, a lucite box was constructed to fit around the pipe housing the source. By placing seeds in two chambers of this box it was possible to get intensities as high as 85,000 r/hr. High dosages could thus be given quickly and conveniently when needed. This reduced the necessity of using the X-ray machine for the high dosage experiments unless a comparison of X-ray and gamma ray effects was wanted. One slight disadvantage of this arrangement, however, was that it caused a small decrease in dose rate in the rest of the field during its use.

Plans are now underway to increase the source to about 2000 curies in 1953 in order that more plants can be grown in the areas of higher radiation and more space will be available at the lower dose rates.

Dosimetry. Dosimetry was performed largely by members of the Health-Physics Department (D. Balber, J. Connolly and J. Nehemias). Readings

were taken on Victoreen ionization chambers as well as with an MX-2 dosimeter and by the film badge method (Ehrlich and Fitch, 1951). There was reasonable agreement between these different methods, but where serious differences existed the film badge values were used. It is realized that absolute values for the exact amount of ionization are extremely difficult to obtain, but it is felt that the dosages reported are probably within 10 per cent. of the true values. However, since the results are largely comparative, small deviations are not considered of much significance as far as our conclusions are concerned. More accurate and definitive calibrations of dose rates are now being undertaken and will be reported elsewhere.

Personnel Safety Precautions. A Co^{60} source of several hundred curies is potentially dangerous and strict safety precautions must be observed. The generally accepted permissible exposure is 50 mr per day or 300 mr per week. All personnel entering the fields were instructed to use film badges and pocket meters (as dosage recorders) and no case of over-exposure has yet occurred.

In order to reduce possible interference with other experiments involving the use or measurement of ionizing radiation and to reduce the possibility

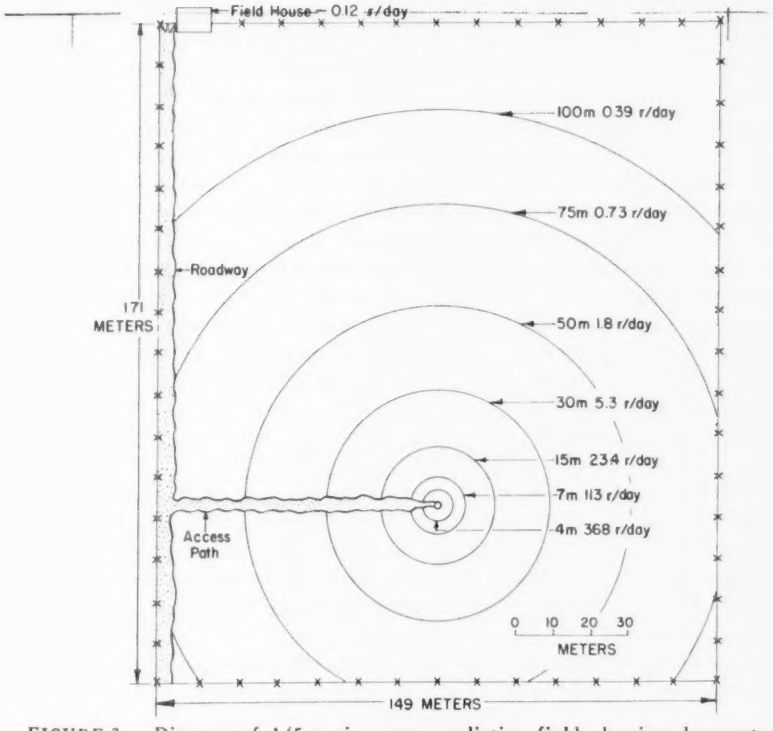

FIGURE 3. Diagram of 145 curie gamma radiation field showing dose rates (roentgens) per day at various distances from the source.

of accidental overexposure of personnel a number of precautions should be taken. The following list of recommendations are based on our experience at Brookhaven and are offered as a guide to those who may wish to set up a similar high intensity radiation field.

1. If possible the field should be located in an isolated area where there is little or no traffic.

2. The immediate growing field should be fenced with a security fence to exclude casual visitors or animals.

3. The fence should be far enough from the source at all points to prevent overexposure of personnel. With the 145 curie source the dose rate at the nearest point of the fence was approximately 60 mr/hr, or slightly more than the daily permissible dose (50 mr) at this laboratory. Thus, for example, a person could work at or near the fence for nearly an hour without overexposure. This has proved to be well within the practical limits for operation of the field. Where longer work periods are required the source must be lowered.

4. There should be an outer fence beyond which personnel can work all day without exceeding the permissible dose. This need not be as high as the inner fence but should be posted at frequent intervals to warn casual visitors.

5. There should be only one point of entrance into the field and this should be kept locked. In the 145 curie field, entrance could be gained only through the control house on the edge of the field which was locked whenever the source was up. The mechanism for lowering the source into the lead shield below the ground as well as a special safety device to prevent personnel from actually entering the radiation field without lowering the source was located in the control house; see diagram, figure 2.

6. A survey meter should be carried into the field when anyone is approaching the source even though all of the mechanical devices are presumably in good working order. The survey meter shows immediately whether or not the source has gone below ground and into the lead shield.

7. All personnel entering the field should be instructed to wear film badges or pocket meters.

EXPERIMENTAL RESULTS

A brief survey of some of the genetic, cytological and morphological effects of chronic irradiation of plants is given on the following pages. These results are in some cases preliminary only but are presented as an indication of the versatility and usefulness of the installation in various radiobiological studies. More detailed reports of the experimental results will be published elsewhere.

Cytological Effects. Plants of *Tradescantia paludosa* L. (strain B2-2) were grown in the 16 curie gamma field in 1949 at various distances from the source and anther smears were examined at various times during the season. The expected types of chromosome aberrations were observed in

TABLE 2

MICRONUCLEI SCORED AT MICROSPORE INTERPHASE AFTER CHRONIC GAMMA IRRADIATION OF *Tradescantia paludosa* (16 CURIE SOURCE IN 1949)

Distance from source in meters	Dosage in r/day	Time of Exposure					
		16 days		32 days		64 days	
		Average No. of mcn† per 100 cells	No. of cells scored	Average No. of mcn† per 100 cells	No. of cells scored	Average No. of mcn† per 100 cells	No. of cells scored
8	7.5	10.70	9,800	11.30	3,196	10.56	4,500
16	1.8	5.16	8,400	3.51	12,600	2.53	6,600
32	0.41	2.32	16,000	1.25	6,400	1.44	7,800
64	0.084	1.92	8,070	0.80	29,600	1.00	6,700
Control	0.00003*	1.78	12,280	0.94	12,000	0.87	23,300

* This is the value of background (naturally occurring) radiation in the control field.

† Mcn = micronuclei.

somatic, meiotic and microspore divisions. However, after preliminary work established that counts of micronuclei in microspore interphase could be used as a measure of chromosome fragmentation (Sparrow, 1950), further study of other stages were not made until 1951 (see p. 36). The numbers of micronuclei observed at microspore interphase after different periods of exposure and at various dose rates are given in table 2.

In order to compare periods of exposure the data from 16, 32 and 64 days were plotted against both total exposure (i.e. dose rate x number of days; fig. 4) and dose rate (fig. 5). It appears from fig. 4 that as the exposure time increases, the number of aberrations (observed as micronuclei) induced

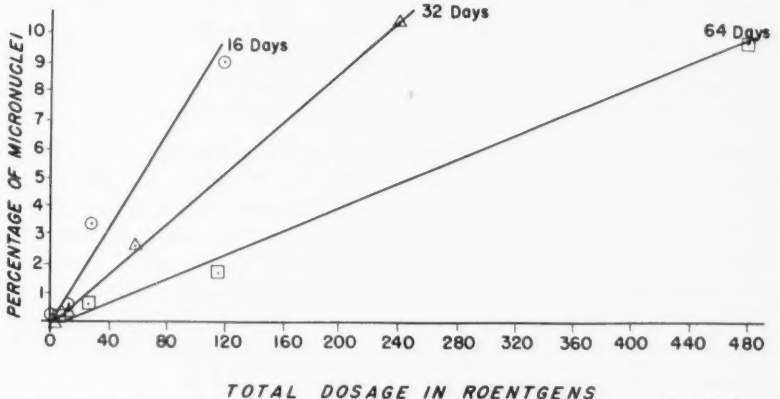

FIGURE 4. Percentage of micronuclei in microspores of *Tradescantia paludosa* after 16, 32 and 64 days exposure plotted against total accumulated dosage.

decreases for a given amount of radiation. However, this *apparent* change in response with length of exposure is not considered to be a real one since the other graph (fig. 5) shows that there is no significant difference between the number of micronuclei scored when the data are plotted against the dose rate. This comparison would indicate that the type of aberrations represented by micronuclei actually are more dependent on the amount of

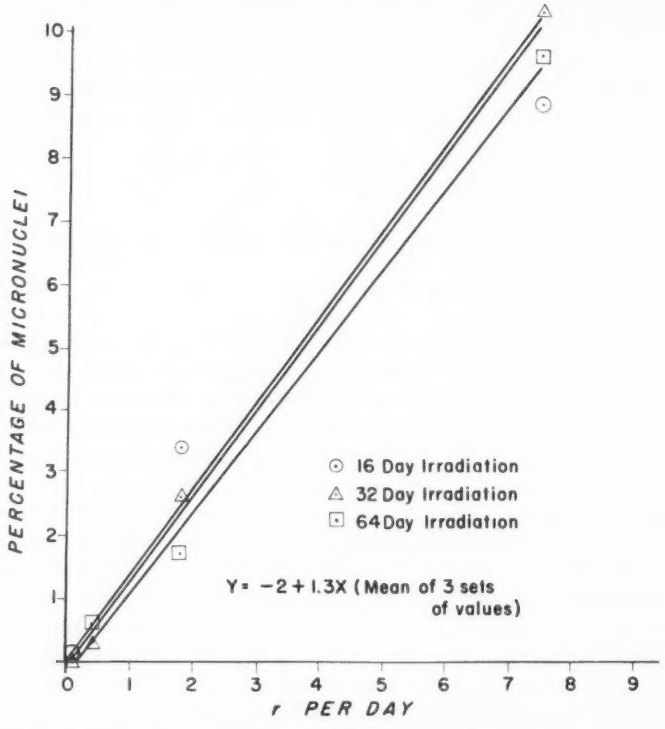

FIGURE 5. Percentage of micronuclei in microspores of *T. paludosa* after 16, 32 and 64 days exposure plotted against dosage in roentgens per day.

radiation received per day (at least after 16 days) than upon the total accumulated dosages. Beyond 16 days the number of aberrations induced at a given dose rate did not increase or decrease significantly (the data from 16 meters showed a significant decrease but this was not found elsewhere and we can offer no satisfactory explanation). These results are in fair agreement with those of Sax (1951) who found chromosome aberrations in Tradescantia microspores to increase after 2- and 3-week exposures to chronic gamma irradiation but no further increase at 3, 4, 6, 11 and 22 weeks.

One of the objectives of the cytological study was to find out what amount of radiation would give a significant increase in chromosome aber-

ration. The data in table 2 show that 0.084 r per day caused no significant increase but that 0.41 r per day (or higher) did show a statistically significant effect (table 2). However, the increase was less than twice that of the control. Since 0.41 r per day of radiation is more than one thousand times greater than the naturally occurring intensity these data do not support the theory that the spontaneously occurring micronuclei are produced by naturally occurring ionizing radiation.

TABLE 3

NUMBER OF FRAGMENTS PRODUCED BY CHRONIC GAMMA IRRADIATION OF *Tradescantia paludosa* (23.4 r PER DAY FOR 47 DAYS)

Stage scored	No. of cells scored	No. of fragments per 100 cells
First meiotic anaphase	600	104.4
Somatic anaphase	871	10.3

In 1951 further cytological studies of somatic and meiotic divisions were made. The number of fragments induced by 23.4 r per day (after 47 days) are given in table 3 for somatic and first meiotic anaphases. The results indicate that under these conditions about 10 times as many fragments are produced in the meiotic cells as in the somatic. The two types of cells are apparently very different in their radiosensitivity, but the cause of the difference is not yet understood (Sparrow, Moses and DuBow, 1952).

GROWTH INHIBITING EFFECT OF RADIATION ON VARIOUS SPECIES OF PLANTS

There was a wide variation in the susceptibility of different plants to injury by the gamma rays. A brief summary of the relative tolerance of the different plants is given in table 4. In addition to growth inhibition of a number of species, some interesting morphological aberrations developed, especially in *Tradescantia paludosa* at the higher dose rates. A more detailed description of these and other morphological abnormalities is given below (see also Gunckel, Sparrow, Morrow and Christensen, 1953).

Corn was also adversely affected by the intense radiation near the 145 curie source. Dosages of 670 r per day were sufficient to kill corn seedlings; although plants moved into the field after pollination grew to the end of the season and produced fairly good ears at this dose rate. Corn plants receiving 368 r per day (4 meters) survived all season although the growth was badly affected (see fig. 6). The total amount of radiation these plants received over a 90-day growing season was approximately 31,000 r. Corn plants that received 230 r per day made a fairly normal growth but produced only 30 per cent. of normal appearing pollen and a very reduced set of seed (fig. 7). These results as well as experiments with acute irradiation indicate that very young corn plants are apparently more sensitive than more mature plants.

TABLE 4

TOLERANCE OF VARIOUS PLANTS TO CHRONIC GAMMA IRRADIATION FROM Co^{60} (RESULTS TENTATIVE ONLY)

Plant	Approximate dosages in r/day and observed effect**		
	No effect	*Mild*	*Severe*
Tradescantia paludosa	15	23	40
Vicia faba	30	60	90
Lilium longiflorum	....	66	150
Melilotus officinalis§	40	100	240
Coleus Blumei	....	100	240
Barley	50	100(?)	....
Nicotiana rustica	50	115	400
Potato	80	....	....
Zea mays	100	250	500
Tomato	100	250	400
Xanthium	125	250	500
Antirrhinum* (4n)	125	250	500
Lupinus albus	160	370	....
Chenopodium album	250	....	600
Kalanchoe Daigremontiana	....	370	1500
Broccoli	300	....	....
Strawberry* ††	400	....	....
Gladiolus* †	400	2,000	....
Digitaria (Crabgrass)*	700	....	....

* The fact that these plants are polyploid may contribute to their higher resistance.

** By effect is meant an obvious effect on size, shape, or vigor of the plants and it should be noted that in most cases only a small number of plants have been grown, especially at the higher dose rates.

† Elizabeth the Queen variety.

†† Varieties Gem and Sparkle.

§ This information supplied by Dr. L. Kavaljian of this department.

Nicotiana rustica was also adversely affected by intense radiation. Fig. 8 shows plants growing at 670, 230, 113 and 2.5 r per day respectively. Below 113 r per day the plants were essentially normal in appearance although height increased out to 25 r per day.

Deleterious Effect of γ-Radiation on Pollen Formation in Zea. Pollen samples were collected from plants of *Zea mays* L. growing in the 16 curie radiation field in 1950. This was done by breaking off a small branch of a tassel just ready to shed. These were fixed and stored in 70 per cent. alcohol until time for examination when grains from single anthers were stained in a 0.2 per cent. solution of iodine potassium-iodide. Normal starch-containing grains stain deeply thus making it possible to distinguish them from grains not properly filled. These were classed as abnormal. Such pollen would probably not function in competition with normal well-filled grains. At 2.5 r per day there was a slight increase over the controls. At higher doses the percentage of abnormal grains increased sharply. Even at 226 r per day there was still 43 per cent. of apparently functional (i.e. nor-

FIGURE 6. Segment of 145 curie field showing growth inhibiting effect on corn at various distances from source (dosages given in table 1). Signs refer to meters from source.

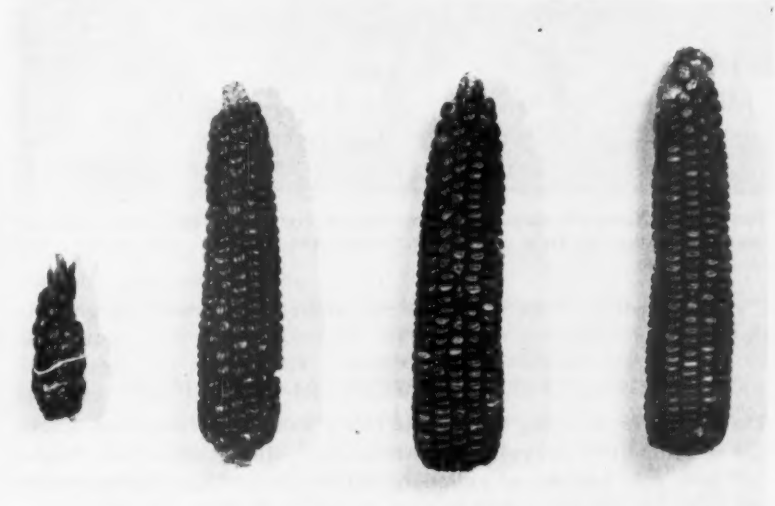

FIGURE 7. Representative ears from various dosage rows showing partial sterility, and loss of vigor at higher dose rates. Dosages were, left to right, 230, 113, 54 and 27 r per day.

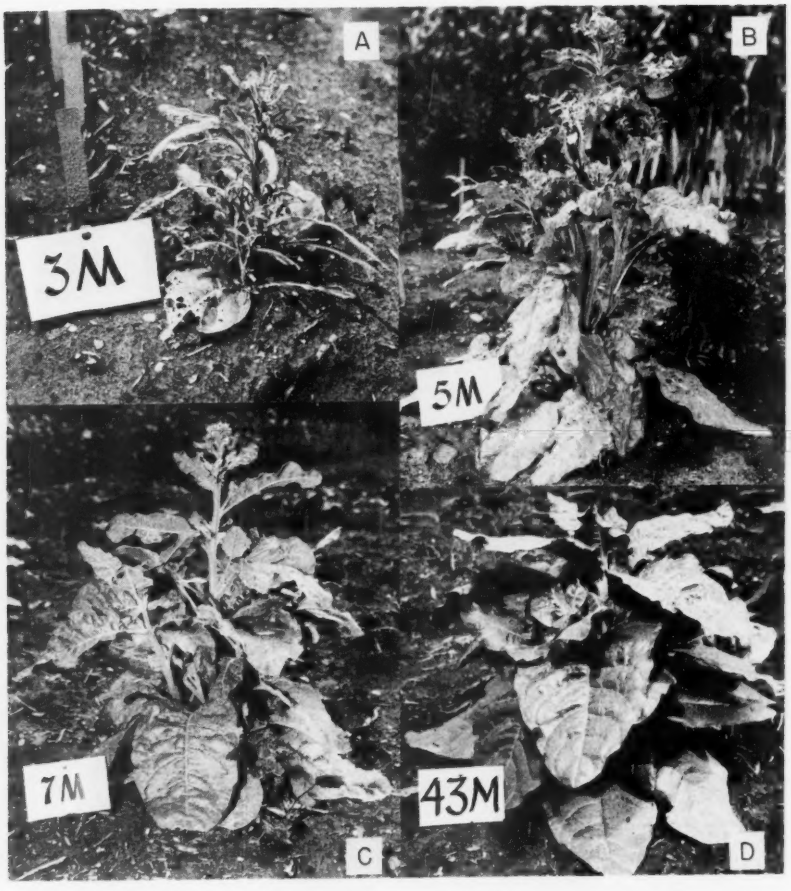

FIGURE 8. *Nicotiana rustica* grown at various distances from 3 meters (3M) to 43 meters from the 145 curie source (for dosages see table 1). Note stunting and abnormal leaves.

mal staining) pollen. The values for the different dose rates are given in table 5.

GENETIC EFFECTS OF CONTINUOUS GAMMA IRRADIATION

The method for studying the genetic effect was to grow dominant stocks in the radiation field and pollinate by recessive pollen produced in a "clean field" with only background radiation. Also pollen of the dominant stock in the gamma field was applied to silks in a clean field.

The mutation rates of four different endosperm (or kernel) characters were studied. Endosperm characters were chosen because they are clearly visible on the ear, they can be scored with ease and certainty, and large num-

TABLE 5

EFFECT OF GAMMA RADIATION FROM A 16 CURIE Co^{60} SOURCE (1950) ON PRODUCTION OF ABNORMAL POLLEN

Meters from source	Approx. dosage r/day	Percentage of normal staining grains
1.5	226	43
2	127	52
3	57	61
4	31.8	69
5	20.2	71
7	10.3	80
10	5.1	87
14	2.54	93
28	0.56	96
40	0.24	95
56	0.11	95
75	0.056	95

bers are readily obtained. The genes studied were *su, pr, sh,* and *r,* located on chromosomes 4, 5, 9 and 10 respectively. The *su* gene is the one causing a kernel to be "sweet," having a wrinkled appearance in the mature stage. The *su* gene is the one in all of the sweet corn used for edible purposes. The *pr* gene (in combination with A, C and R, basic color genes of the kernel) causes kernels to be red instead of dark blue or purple when *Pr* is present.

The gene *sh* causes kernels to be decidedly shrunken due to a lack of complete starch formation in the kernel. The gene *r,* one of the three basic kernel color genes, causes a colorless kernel instead of one deeply pigmented with purple or red.

Normally when pollen of a dominant stock is placed upon silks of a recessive stock, the kernels formed will all be like the dominant stock. In the case of the four characters being studied the kernels, with exception of mutations, were all plump (due to the *Su* and *Sh* genes), were fully colored due to the *R* gene and were purple due to the *Pr* gene. Mutations to recessives at the four loci usually occurred singly and not in combination with any other mutant gene.

Ears of crosses of recessive by dominant were examined after harvest and drying. Since each good ear represents a population of several hundred seeds, large numbers essential for a mutation study are readily obtained. The 1950 data represent approximately 275,000 seeds. Counting such a number of seeds would be a considerable chore. Reliable estimates can be obtained by shelling the ears, cleaning the seed, weighing and counting several aliquot samples.

From the 1950 crop the following results were obtained (see table 6 and figure 9):

1. There was no increase in mutation over the control when the radiation was less than 5 r/day.

TABLE 6

MICROSPORE MUTATIONS (x 10^{-4}) PRODUCED IN 1950 RADIATION EXPERIMENT

Distance from source (meters)	Dosage per day in roentgens	Mutations in genes studied				Total counted
		su	*sh*	*pr*	*r*	
2	127	128	100	141	164	6,400
3	57	20.7	17.2	20.7	58.6	8,700
4	31.8	7.5	3.1	16.9	33.8	16,100
5	20.2	7.6	2.9	14.8	29.5	21,000
7	10.3	0	4.5	7.5	23.9	6,700
10	5.1	2.2	2.2	6.5	17.2	9,300
14	2.5	2.9	1.4	2.4	15.3	41,700
20	1.3	5.0	4.1	3.8	19.1	32,000
28	0.56	2.6	2.9	3.7	18.0	38,300
40	0.24	2.7	2.0	6.1	19.0	14,700
57	0.11	0	1.0	4.1	14.3	9,800
75	0.056	2.3	0.9	4.6	18.1	70,200
Total seeds						274,900
Control (field pollinated)		0	1.8	3.6	14.5	16,500
Control (hand pollinated)		0	3.2	4.8	33.9	6,200
1949 results (30.4 to .27r/day)		1.9	1.1	3.0	16.3	52,600

2. Above 5 r/day there was a gradual increase to 32 r/day with a more marked increase from 32–57 r/day. Above 57 r/day the increase was even more marked. The increase in mutations observed at the higher dose rates was greater than expected if the increase is linearly proportional to dose.

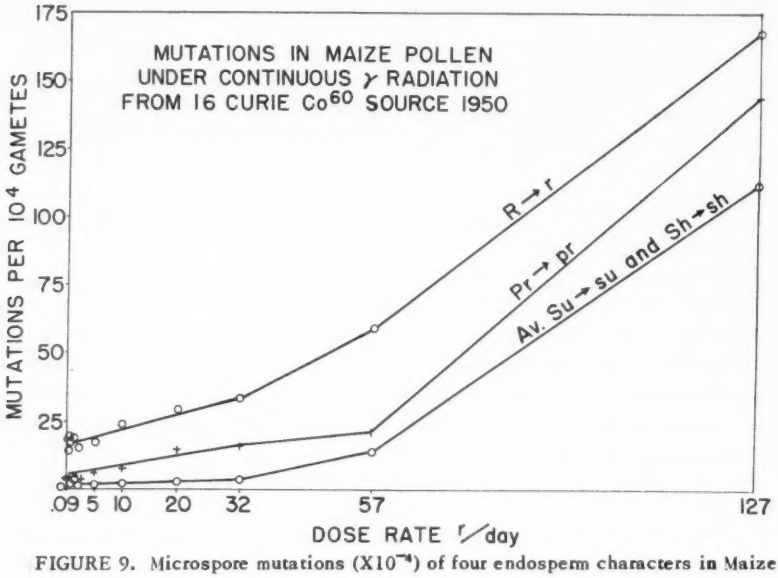

FIGURE 9. Microspore mutations ($X10^{-4}$) of four endosperm characters in Maize.

3. The logarithm of the mutation rate was linearly proportional to dose rate.

4. The gene with the greatest spontaneous frequency (R) showed a smaller percentage increase in induced changes than Su, Sh and Pr (Singleton, 1951).

MORPHOLOGICAL AND HISTOLOGICAL RESPONSE

Dr. J. E. Gunckel and Miss Eileen Morrow of Rutgers University have collaborated with the authors during the past two summers.[1] The following report was prepared by Dr. Gunckel:

A number of histological and morphological changes have been noted in plants after exposures to continuous gamma irradiation. The response varied considerably, depending upon dose rate, duration of exposure, the particular species observed, the age or the stage of development of plant parts irradiated, and upon the physiological condition of the plants (Gunckel et al., 1953b).

Two of the most striking histological effects of irradiation were upon leaves or leaf development (Gunckel et al., 1953a) and upon flowering. Depending upon the plants observed, both flower and leaf formation fell into several different categories.

In tomato (haploid, diploid, and tetraploid), Xanthium, Vicia, and lupine plants, flower formation was completely inhibited by high dose rates (about 500 r/day). Limited numbers of sterile flowers occurred at lower dose rates. Snapdragon plants (tetraploid) were slightly less affected, whereas strawberry flowering and general appearance were completely normal up to 400 r/day (see also table 4).

In Xanthium, leaves already present on the plant at the time of transplanting to the gamma field retained their normal cordate to ovate form between 500 and 250 r/day, but the leaf texture was altered, becoming stiff, dry and coarse, and there was a crinkling of the leaves due to proliferation of mesophyll cells after vein growth had ceased. Younger leaves were linear and with ragged lobing due to failure of the plate meristems to develop. The leaves did not alter appreciably in thickness. Abnormal clustering of the flowers and fruit occurred at 250 r but not at 125 r (fig. 12 A and B). At 500 r/day flowers did not develop.

Both old and young leaves of snapdragon plants (tetraploid) receiving between 500 r and 60 r per day did not alter in shape but became progressively thickened and of a leathery texture. Sections of the leaves showed that the progressive thickening was due to repeated division of the palisade cells and by over-all cell enlargement.

Leaves from tobacco *(N. rustica)* showed still another pattern of abnormal leaf development. Both older and younger leaves showed a marked inhibition of plate rib meristem activity between 670 r and 67 r so that the normally ovate leaves were markedly linear. Between 67 r and 43 r older

[1]Work done in part under contract No. AT(30-1)-1120 with the U.S.A.E.C.

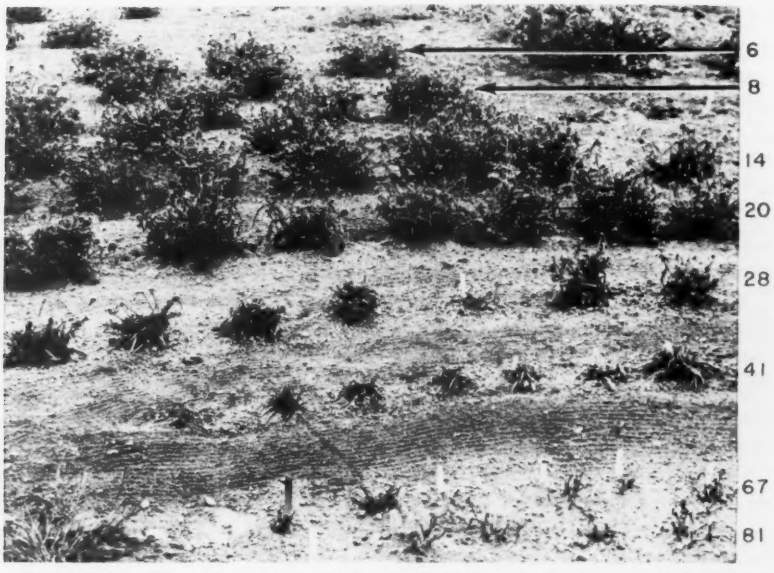

FIGURE 10. View of segment of 16-curie field (1950) showing growth-inhibiting effect on *Tradescantia paludosa* after 114 days exposure. Values given are in roentgens per day.

leaves appeared normal but crinkling and proliferation of the mesophyll cells between the veins was apparent in younger leaves. Sections through the leaves showed a marked thickening of the blades at higher dosages due not to cell proliferation but to slight cell enlargement and to a pulling apart of the mesophyll cells which disrupted the organization of mesophyll especially at the leaf margin.

Rooted cuttings of *Tradescantia paludosa* receiving dosages varying from 113 r to about 2 r per day show varying responses from almost complete growth inhibition at the higher dose rates to apparently normal plants at the lower (fig. 10). There is a critical dosage range between about 37 r and 12.7 r per day in which a marked proliferation and overgrowth of flower heads and many abnormal axillary buds occur.

Overgrowth of flower heads is by the proliferation of many bracteoles and by leaf-like structures in floral positions. Further flower parts may be variously modified as by loss of parts, particularly of sepals, anthers, and stigmatic surfaces, or have extra petals or half-petals bearing half anthers.

Normally, the first to third axillary buds grow out into a solitary flowering stalk, and buds at lower nodes are inhibited (fig. 11A). In the critical range cited, however, from four to five axillary buds develop shoots which have very short internodes and a mass of fused and dissected leaves (fig. 11B). These usually grow out into modified single or multiple vegetative shoots and send out a short flower stalk bearing normal flower heads which

may later show some of the overgrowth already described (fig. 11C and D). Cuttings from these irradiated plants eventually grow normally, indicating that the abnormalities observed are probably due to physiological disturbances rather than to mutation.

Suppression of Crown-gall Formation in Tomatoes. Dr. A. E. Dimond of the Connecticut Agricultural Experiment Station, New Haven, has been studying the effect of gamma radiation upon certain plant diseases and the

FIGURE 11. A. Normal shoot and inflorescence of *T. paludosa.* B. Shoot showing effect of exposure to approximately 37 r per day for approximately 119 days. C and D. Abnormal growth with multiple shoots on plants recovering from chronic exposure to 30 r per day.

FIGURE 12. A. Abnormal leaves and seed cluster from Xanthium exposed for 76 days at 230 r per day. B. Plant exposed same length of time at 60 r per day which appears normal.

relation between the host and parasite under radiation in the 16 curie and 145 curie fields. Interesting information has been obtained on crown gall formation in tomatoes. It was found that 30,000 r of gamma rays delivered at 80 r/hour prevented the formation of galls on tomato plants inoculated with *Agrobacterium tumefaciens*. However, cultures of these bacteria subjected to 50,000 r of gamma radiation (at 80 r/hour) still produced normal galls in non-irradiated plants. Dimond (1951) concludes that "the extent of gall suppression is a measure of radiation damage to a host, and probably results in part from a decrease in ability of the plant to undergo chromosomal and cell division and cell enlargement."

ACKNOWLEDGEMENTS

The advice or assistance of a number of people in planning and operating the installation is acknowledged: planning—Dr. L. F. Nims, David Balber, George Stoneman and Arnold Runge; operation—Eric Christensen and Frank German; handling of sources and measurement of dosage—David Balber, J. Connelly and J. Nehemias; technical assistance—Eric Christensen, Mrs. G. Davison, Mrs. R. Sparrow, David Matthews, Misses Virginia Pond and Mary Koester; statistical analysis—Dr. A. E. Brandt.

SUMMARY

Radiocobalt has been used as a source of gamma rays in a study of the effect of chronic irradiation on growing plants. The installation and method of operation of sources of approximately 16 and 145 curies is described. The Co^{60} was placed in the center of an experimental plot in such a fashion that it could be operated safely by remote control. By placing plants in concentric circles (or arcs) around the source at various distances it was possible to study the effects of a wide range of radiation intensities. Actual dosages used varied from less than 0.1 r per day up to dosages in excess of 2,000 r per day. The tolerance to ionizing radiation of different species of plants studied varied widely. Preliminary tolerances are given for nineteen different species of plants. *Tradescantia paludosa* showed severe effects at 30 r per day, whereas Gladiolus showed relatively little effect after 2,000 r per day for 42 days.

Mutation rates of four endosperm characters of corn revealed the following: (1) There was no increase in mutation rate over the control when the radiation was less than 5 r/day. (2) Above 5 r/day there was a gradual increase up to 31 r/day with a more marked increase from 32 to 57 r/day. From 57 r/day to 127 r/day the increase in mutation rate was even more marked. The increase in mutation rate at the higher intensities of radiation was greater than expected if the increase is linearly proportional to dose. (3) The logarithm of the mutation rate seemed to show a linear relationship with dose received. (4) The gene with the greatest spontaneous mutation frequency *(R)* showed a smaller percentage increase in induced changes than the other three genes *Su, Sh* and *Pr*.

Under chronic gamma radiation the percentage of abnormal pollen grains in corn increased with an increase in radiation. There was no marked increase over the control below 2.6 r/day and the maximum effect noted was 57 per cent. abnormal grains at 226 r/day.

Chromosome fragments were scored in somatic and meiotic (first) anaphase of Tradescantia after 47 days exposure. Fragmentation in meiosis was more than tenfold greater than that observed in somatic cells. Micronuclei derived from chromosome breaks were scored in microspores of chronically exposed Tradescantia. A statistically significant increase in number of micronuclei was found at a dose rate as low as 0.41 r per day. The numbers of micronuclei did not increase significantly after 32 and 64 days as compared to that found after 16 days.

Other effects observed included killing, various degrees of growth inhibition, inhibition of flowering, pollen abortion, reduced fertility (or complete sterility in some cases) abnormal growth pattern of both floral and vegetative parts as well as a strong tendency to proliferative growth in some cases. The effect of irradiation on production of crown gall in tomatoes is also briefly reported.

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COLOR RESPONSES IN THE CLADOCERA AND THEIR ECOLOGICAL SIGNIFICANCE

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Light has long been recognized as an important ecological factor in the Cladocera (see Welch, 1952). The existence of elaborate mechanistic behavior patterns in certain of the arthropoda is well known. The experiments to be reported here demonstrate the degree to which light cues have been exploited in the evolution of the complicated behavior of the Cladocera, a degree of exploitation hitherto unsuspected. The concepts to be introduced raise at once the question of their ubiquity and the possibility of variant patterns.

Most of these studies were made in one gallon aquaria. It is extremely important that reflections be eliminated from the glass surfaces. For use with vertical lighting the sides, back, and bottom were coated inside with a mixture of beeswax, resin, and lampblack; for use with lateral lighting one of the sides was left clear. While this coating is not particularly durable, it is not toxic and is easily repaired.

The various filters used in front of microscope lamps must have known transmission spectra. For this work a set of Corning color filters is indispensable. Since most neutral-density filters do not cut off exactly the same amount of all wave lengths, the best kinds for this work are pieces of cheesecloth or fine wire screening painted flat black. A Beckman Model B spectrophotometer was used to analyze the various filters. With the photocell and cuvette carriage removed, it also served as a source of relatively monochromatic light for direct use on the animals. Once a monochromatic analysis is made of a particular light response, it is possible to use a filter which will transmit much of the appropriate light and little or none of other wave lengths. Less accurate use of wave length in studies of this kind can lead to serious error.

Most of the experiments were made on summer populations of *Daphnia magna* (Straus). Other species of Cladocera will be indicated where used.

EVIDENCE OF COLOR RESPONSE

If Cladocera are placed in a vertical beam of light where the wave length is controlled with color filters or by using a monochrometer they will swim up into the light if the wave length is changed from less than 5000 Å to more than 5000 Å, and down with some degree of brief lateral scattering on the reverse change. This is usually a mixed response to both a change in color and intensity, in which the blue or violet light is apparently brighter to the organisms than the red, yellow, or green light. F. A. Brown, Jr. (personal communication), has found simple evidence that color sensi-

tivity is involved, in a phenomenon similar to the after-image effect in human vision. When the light is changed from yellow to white, a blue response occurs (down-swimming), and when it is changed from blue to white a yellow response occurs (up-swimming). Since both responses accompany an increase in brightness, intensity cannot be the sole cause of the response. This response to color change has been observed by us in all the Cladocera we have examined, including: *Sida crystallina* (Müller), *Daphnia magna* (Straus), *Daphnia longispina hyalina* (Leydig), *Simocephalus vetulus* (Müller), *Simocephalus serrulatus* (Koch), *Ceriodaphnia reticulata* (Jurine), *Moina affinis* (Birge), *Bosmina obtusirostris* (Sars), *Kurzia latissima* (Kurz), *Chydorus globosus* (Baird), and *Leptodora kindtii* (Focke). Some variations in response to color are as follows: Moina is unusually sensitive to blue, being almost paralyzed by sudden exposure, and Ceriodaphnia precedes all of its responses with a considerable time lag.

Preliminary analysis with a monochrometer has indicated the approximate wave lengths that are active in this two color response pattern. The technique is as follows: A population of Cladocera in a small container is illuminated by two light sources intersecting at right angles, a vertical light beam from a microscope lamp having appropriate slits and filters, and the other a horizontal light beam emerging from the slit of a monochrometer. It is then possible to restrict the vertical beam to long wave lengths and to add successively shorter wave lengths from the monochrometer, and to restrict the vertical beam to short wave lengths and to add successively longer wave lengths from the monochrometer. The vertical shaft serves to hold the population in place while the horizontal beam is off, and also lessens the difficulties entailed by sudden changes in intensity. Furthermore, since adding light from the monochrometer always constitutes an increase in light, it is impossible to attribute its effect to a decrease in total energy.

When the vertical beam is restricted to long wave lengths, the addition of short wave lengths produces a dropping or sinking effect in the population, either by weakening the swimming effort or by causing active down-swimming. No drop effect on *D. magna* is found above 5500 Å, while a maximal dropping is found from 4500 Å down to at least 3500 Å. Between 5500 Å and 4500 Å partial responses occur.

When the vertical beam is restricted to short wave lengths and successively longer wave lengths are added from the monochrometer, partial rises (feeble up-swimming) begin to appear at 4700 Å, and are maximal at 5700 Å. They disappear again at about 6800 Å. Although the wave lengths at which these effects occur may vary somewhat from species to species of Cladocera, we have not yet encountered any great variation. Other analyses have revealed nothing to indicate more than a two color response pattern in this group.

THE COLOR DANCES

The most convincing evidence that Cladocera respond to the wave length of light is seen in their behavior when continuously illuminated by either

short or long wave lengths. This behavior is seen best with a light source from above giving a uniform intensity over the entire aquarium. Under red light (6000 Å or over) the population appears calm, the individuals dancing upright in the water, with a small horizontal vector in their locomotion. The vertical vector is larger and varies somewhat throughout the population. Under blue light (5000 Å or under) the population is distinctly agitated, the individuals leaning well forward in their dance and roaming about with a large horizontal vector to their locomotion. Prolonged exposure to this light has literally driven populations to death.

Moving the light shows that the color dances are oriented, not to gravity, but to the direction of propagation of the light. The largest vector and hence the direction of locomotion in the blue dance is always oriented at right angles to the line of propagation of the light, while the largest vector in the red dance is always directed parallel to the line of propagation of the light. When blue light is introduced from the side a vigorous wandering occurs in all directions in the vertical plane perpendicular to the light; when red light is introduced from the side the red dance remains a quiescent dance with a predominant vector, if any, in a line parallel to the direction of the light, swimming slowly away from the light and returning somewhat more rapidly at irregular intervals.

Under white light from above the dances are discrete; at any one moment an individual is either red-dancing or blue-dancing. If the proportion of energy in the short wave lengths is too high, all the animals will blue-dance all the time; if the proportion of energy in the long wave lengths is too high all the animals will red-dance all the time. Within a range of proportions specific for each species, and probably affected by several environmental factors, the individuals will change spontaneously back and forth from one dance to the other. The total proportion of time spent doing each of the dances is extremely sensitive to the proportional energies of short and long wave lengths present.

These color dances have been observed wherever we have looked for them in the dancing forms: *Daphnia magna,* Ceriodaphnia, Moina, and *Bosmina.*

EFFECTS OF INTENSITY

The effect of a change in intensity is partially color specific. With vertical lighting, dimming either a blue or a red light causes the population to swim up, especially as the light becomes extremely dim. Brightening a blue light will cause the organisms to swim actively down, but no degree or suddenness of brightening of a yellow light will cause the population to spread itself more than slightly downward. Daphnia are agitated by intensity changes, and are more active in dim than in bright light.

In 15 to 20 minutes Cladocera adapt considerably to various intensities. Under vertical light the only differences in the dances after adaptation to an intensity change are the positions of the populations. Although both color dances persist as distinct types of locomotion, most of the population

may be found toward the top of the tank in dim light, or toward the bottom in bright light. Given enough time, these differences all but disappear.

The repeated reversal of direction of locomotion seen in the red dance, especially with light from the side, suggest that the intensity gradient in the water is an important controlling factor in this type of locomotion. Slowly brightening a lateral red light, using a variable transformer, will cause the individuals to persist in their measured jogging away from the light, while slowly dimming the same light will induce them to switch back on the more rapid return journey. Proper manipulation of the intensity can synchronize the locomotion of the entire population.

The movements of the blue dance do not suggest any obvious relation to an intensity gradient. Whenever the intensity of a blue light is changed the dance is interrupted.

EFFECT OF TEMPERATURE

When *Daphnia magna,* adapted to 25° C., are cooled to 10° C. or lower the blue response disappears. While the organisms still respond to the full spectrum, they respond as though it were all red light. The intensity effects still persist, but the animal behaves as though the light were red, and cannot be made to swim downward by sudden exposure to a bright blue light. If the intensity factor is eliminated in changing from red to blue light no response occurs.

The completeness of this "color blindness" in the cold is seen in the dances: under any color or intensity of light whatsoever the only dance is the red dance. In animals kept below 10° C. for several weeks the blue response is still absent.

The effect of temperature is rapid. In a matter of seconds a cooled Daphnia loses its blue response, and regains it with equal facility upon being warmed.

DISCUSSION

While these studies are preliminary, and many of the more subtle effects remain to be explored, the phenomena described allow some degree of interpretation and speculation.

The color dances combine to form a suitable mechanism for concentrating a cladoceran population in areas of denser phytoplankton. This concentration mechanism can succeed only in the absence of perceptible changes in brightness. Thus, while a cladoceran will turn back as it passes under the shadow of a floating leaf, it will apparently not notice the difference as it passes into water slightly more dense in phytoplankton; it will enter such an area or leave with no visible effort to stay in one place or the other.

Yet the organisms are orienting to the light components in a statistical manner that is far more sensitive than simple perception. The time spent in the red dance versus that in the blue dance is variable, but averages out to be highly sensitive to the relative intensities of wave lengths

present. Since green phytoplankton filters out more of the short wave lengths than of the long wave lengths, the total time spent red-dancing becomes greater as the individual swims into areas of denser food. The red dance, having a small horizontal vector, keeps the individual in place, while the blue dance, with its large horizontal vector, promotes considerable wandering. The end result is that more time is spent by the individual in the areas of greater food; hence, a concentration of the population occurs at that place.

A demonstration of this mechanism is possible using a shallow (¼ inch deep) partitioned lucite tray over the aquarium. If the partitions are filled alternately with clear water and algal suspensions, the population will tend to congregate (and show more red dancing) beneath their food. It is possible, by using more and more dense suspensions of algae, to get *D. magna* four times as concentrated under the phytoplankton as under clear water, before the decrease in intensity overrules and the areas beneath the food are avoided. This demonstration has also succeeded with *Bosmina obtusirostris*.

The light must be adjusted for each particular species so that both dances occur. This light mixture is different for different species, being relatively blue for Bosmina and decidedly yellow for Moina.

While some of the theories advanced to explain diurnal migrations are suited to some of the observed patterns, a considerable residue is left for which a satisfactory explanation is wanting. This is especially true of the Cladocera. Professor G. E. Hutchinson of Yale University has collected a wealth of information both on the theories and on field information, which will appear in his forthcoming text on limnology.

Some of the color phenomena offer new explanations for migrations. These phenomena are:

1. Dimming either color can provoke up-swimming
2. Brightening wave lengths shorter than 5000 Å can provoke down-swimming.
3. Brightening wave lengths longer than 5000 Å cannot provoke down-swimming, but may cause a slow spread downward.
4. Shifting the spectrum of light toward blue without changing the intensity can provoke down-swimming.
5. Shifting the spectrum of light toward red without a change in intensity can provoke up-swimming.
6. Cooling below 10° C. can mask all of the blue responses, leaving red responses at all wave lengths.
7. Adaptations of the response mechanism to (1), (2), and (3) are more rapid and less limited than those to (4) and (5); adaptation to (6) was not found after several weeks.

In clear lakes the proportions of wave lengths above and below 5000 Å do not change appreciably with depth. A thermocline can, however, eliminate blue responses below a particular level. A population may be forced down at dawn until it reaches the thermocline, cools, and loses its blue response. At dusk all of the individuals, whether in cold water and temporarily "color blind" or not, can be pulled up as the intensity falls. Such organisms probably would not migrate in winter.

This type of diurnal migration has been accomplished with *D. magna* in a glass cylinder two feet high, the bottom half of which is immersed in ice water in a larger glass cylinder. As a vertical light over the cylinder is slowly brightened, the population swims down, usually in descending blue dances. Soon the lower members reach the thermocline, where the dance immediately assumes red characteristics and no further down-swimming occurs. Continued brightening will ultimately force the entire population into the thermocline. Under sustained brightness various individuals swim up through the thermocline, but in a matter of seconds they recover their blue responses and return. As the vertical light is dimmed the entire population can be pulled to the surface.

This experiment works equally well with white or blue light, but works very poorly with wave lengths over 5000 Å.

Evidence that no other barrier restricts the population at the thermocline is shown by moving the light down to the bottom on one side of the cylinder. The population follows the light, swimming down without hesitation into the cold water. When the light is returned to above, those individuals not narcotized by the cold will return as far as the thermocline.

In lakes with various substances that selectively remove blue light (stains, clays, phytoplankton, etc.) the amplitude of migration may be controlled by the relative decrease in the intensity of short wave lengths with depth. Experiments with various intensities of the two color components suggest that the tolerable proportion of energy in the short wave lengths falls as the total intensity increases. Species with such a response pattern would seek lower depths during the day, rising again at night. If the light components were changing rapidly with depth, the level of the population at any one time could well be a restricted zone. The slowness of adaptation to color relative to that to intensity indicates that a color gradient in the water would be fully as likely to control migration as a simple intensity gradient. In any event, the two operate in the same direction and probably both are used.

Organisms responding only to the proportions of energy in the various wave lengths, irrespective of the total spectral intensity, would be expected to rise briefly at sunrise and again at sunset, periods when the proportion of yellow light in the spectrum is greatest.

Further combinations of these and other phenomena may serve to explain other patterns of migration. It is evident that the light reactions behind these phenomena are more complex than has been anticipated.

The orientation of Cladocera to polarized light is being reported elsewhere, but the interrelation of that phenomenon to these on color and intensity will have to be analyzed, especially with reference to post-twilight and pre-dawn plankton migrations (when the proportion of blue polarized light is highest).

The organs that receive the different stimuli remain to be determined. It should be pointed out that, although we have spoken consistently of two-color vision, a system having one photoreceptor sensitive to the entire

light spectrum (an intensity receptor), and one sensitive only to short wave lengths (a color receptor) will satisfy all of the evidence.

SUMMARY

Cladocera respond to changes in the wave length of vertical light by swimming up when the energy is shifted toward the long end of the spectrum (over 5000Å), and by swimming down when the energy is shifted toward the short end of the spectrum (under 5000 Å). Specific behavior patterns (color dances) are observed under sustained long or short wave lengths. Responses to changes in intensity are described in relation to the two colors. Temperatures less than 10° C. eliminate all aspects of the "blue" response, leaving a "red" response in its place. The color dances are shown to provide a probability mechanism for concentrating populations in areas of dense phytoplankton. Responses to changes in color together with responses to changes in intensity and the effect of temperature, are shown to be intimately associated with diurnal migration.

LITERATURE CITED

Welch, Paul S., 1952, Limnology. 2nd edition. New York, McGraw Hill.

PUBLICATIONS RECEIVED

THE AMERICAN NATURALIST is glad to acknowledge here the receipt of books on biological and natural history subjects which are likely to be of interest to our readers. No undertaking to publish reviews is implied in this acknowledgment. Books for notice may be sent to:

EDITORIAL OFFICE
The American Naturalist
635 W. 247 St.
New York 71, N. Y.

Dawes, Ben, 1952. A hundred years of biology. 429 p., ill. $5.00. Duckworth and Company, Ltd., London, and The Macmillan Company, New York.

This will be a useful book, because it is a sort of annotated bibliography, a guide to many highways and byways in modern biology. It is too choppy, too burdened with names and disconnected ideas, however, to serve the general reader or the beginning student; and many specialists will feel that the treatment of their speciality is inadequate or misleading. It is, however, a brave summary of a wide field, particularly successful in weaving botanical and zoological ideas into a biological pattern. The stress on British workers and institutions is understandable; these have played a leading role in biology during the last hundred years.

M.B.

Dice, Lee R., 1952. Natural communities. 547 p., ill. $5.50. University of Michigan Press, Ann Arbor, Michigan.

Only three years after the publication of the monumental "Principles of Animal Ecology" by Allee, Emerson, Park, Park, and Schmidt, the book of Professor Dice gives a fresh account of the branch of ecology known as "synecology" or "community ecology." The presentation is simple and assumes a familiarity with only the elementary principles of biology on the part of the reader.

T.D.

Fisher, Walter Kenrick, 1952. The Sipunculid worms of California and Baja California. No. 3306, From Proceedings of the United States National Museum, Vol. 102, pp. 371-450., ill. Smithsonian Institution, Washington, D. C.

Gowen, John W., 1952. Heterosis. 552 p., ill. $5.75. Iowa State College Press, Ames, Iowa.

Kohler, Fred, 1952. Evolution and human destiny. 120 p., $2.75. Philosophical Library, New York.

The author, who is not primarily a biologist, discovers evolution and hastens to explain it to others. In so doing he expresses some interest-

ing ideas as well as ideas which are no longer new and known to be invalid.

T.D.

Lemmon, R. S., 1952. Our amazing birds. 240 p., 102 illustrations by Don R. Eckelberry. $3.95. Doubleday and Co., New York.

A beautifully written, illustrated, and produced book of chit-chat about 102 American birds. There is not a Latin name in the 240 pages but instead a lot of news and views about bird character and personality. The paintings in black and white by Don Eckelberry are especially decorative.

L.C.D.

Linder, Folke, 1952. Contributions to the morphology and taxonomy of the Branchiopoda notostraca, with special reference to the North American species. No. 3291, From Proceedings of the United States National Museum, Vol. 102, pp. 1-69, ill. Smithsonian Institution, Washington, D. C. U. S. Government Printing Office, Washington, D. C.

Montagu, M. F. Ashley, 1952. Darwin. Competition and cooperation. 148 p., $2.50. Henry Schuman, New York.

The worthy purpose of this book is "to induce a better understanding of the significance of certain aspects of Darwinism," and thus to combat its misuse by race and class bigots. Together with Kropotkin, to whose memory the book is dedicated, the author stresses the evolutionary importance of mutual aid and cooperation as opposed to the struggle for existence and competition emphasized by Darwin and many of his followers. The argument is presented in an easy but forceful style; its effectiveness would have been enhanced if it did not in places suggest special pleading.

T.D.

Roe, Anne, 1951. A psychological study of eminent biologists. 68 p. $2.00. Psychological Monographs, Vol. 65, No. 14 (Whole No. 331). The American Psychological Association, Washington 5, D. C.

Sailer, R. I., 1952. A review of the stink bugs of the genus Mecidea. Proceedings of the United States National Museum, Smithsonian Institution, Vol. 102, No. 3309, pp. 471-505. U. S. Government Printing Office, Washington, D. C.

Silva, Paul C., 1952. A review of nomenclatural conservation in the algae from the point of view of the type method. University of California Publications in Botany, Vol. 25, No. 4, pp. 241-324. $1.25. University of California Press, Berkeley, California.

Wagner, Warren H., Jr., 1952. The fern genus Diellia. 212 p., ill. $3.00. University of California Publications in Botany, Vol. 26, No. 1. University of California Press, Berkeley, California.

THE AMERICAN SOCIETY OF NATURALISTS

SECRETARY'S REPORT, 1952

During the past year the Society took part in arranging two symposia, one held at the meeting of the American Institute of Biological Sciences, in Minneapolis in September, 1951, and cosponsored by the Genetics Society of America; and the second, sponsored jointly with the Biometric Society (Eastern Section) and Section H (Anthropology) at the meeting of the American Association for the Advancement of Science in Philadelphia on December 27, 1951. In the latter symposium on "The use of statistical models to interpret data on human population genetics" (Chairman, Marian W. Smith), the speakers were as follows:

General Introduction to the Theory and Methods of Human Population Genetics. C. C. Li, University of Pittsburgh

Methods and Materials for the Estimation of Mutation Rates in Man, J. V. Neel, University of Michigan

Methods and Materials for Estimating Genetic Drift in Man, Bentley Glass, Johns Hopkins University

Methods and Materials for Determining the System of Mating in Contemporary Human Populations, J. N. Spuhler, University of Michigan; D. J. Hager, Princeton University

Summary and Discussion, Howard Levene, Columbia University

Inasmuch as the AIBS and the AAAS have arranged in coming years to meet always in different parts of the country as well as at different seasons of the year, it seems very desirable to continue the practice of assisting to arrange symposia at both meetings. This provides a greater diversity of subjects and an opportunity for those members who cannot attend one meeting to find something planned by the Society at the other. Thus, in the current year, in addition to the symposium held at the AIBS meeting in Ithaca, the program of which is given below, a symposium has been arranged jointly with AAAS Section G (Botany) and the Illinois Section of the American Society of Plant Physiologists, on the general subject of "Nitrogen Metabolism in the Green Plant."

The annual business meeting of the Society took place on September 10, 1952, in the auditorium of Van Rensselaer Hall, Cornell University, Ithaca, New York. The annual symposium, cosponsored by the Society for the Study of Evolution, the Genetics Society of America, and the American Society of Zoologists, had been held in the same place on the afternoon of September 8, and was, like the address of the President of the Society on Tuesday evening, September 9, exceptionally well attended. The Symposium, on "Biochemical Evolution," was as follows:

Widening Horizons. Harold F. Blum, Princeton University, Princeton.

Inventions in Iron Metabolism. Sam Granick, Rockefeller Institute for Medical Research, New York

Some Implications of the Coacervate Theory of Life. U. N. Lanham, University of Michigan, Ann Arbor

Biochemical Characters of Supraspecific Categories in Animals. Marcel Florkin, University of Liege, Belgium

The President's address was given by Professor Sewall Wright, of the University of Chicago, on the subject "Gene and Organism," and it excited widespread comment.

During the past year the work of the Secretary was again focussed on increasing the active membership of the Society to compensate for the annual losses due to death, retirement, or resignation, and in addition to allow a modest growth in keeping with the aims and standards of the Society. Last year in September the Secretary reported 424 active members, 156 emeritus members, and 10 honorary members. The membership was increased by 50 following the elections at the Minneapolis meeting. During the year six deaths were reported (two emeritus members, four active members), there were fourteen resignations, and six active members became emeritus. At the time of the annual meeting in 1952 there were therefore 450 active members, 160 emeritus members, and 10 honorary members, a total membership of 620. It is thus encouraging to report that the Society is now back to the size it had attained in 1949, just prior to the assumption of editorial control of *The American Naturalist* and the increase in dues necessary to include subscription to the journal. However, it should be noted that in spite of the increased election of new members, the percentage of emeritus members is still at an all-time peak (27.4 per cent), and the percentage of active members is still insufficient to finance and maintain the work of the Society.

Contrary to what some members appear to think, there has been no alteration of the standards required for election to membership in the Society. The same procedure for nomination to membership, the same criteria of broad biological interests and continuous productivity in research, and the same careful consideration of each nominee by the Executive Committee have been maintained. However, it is imperative for the Society to face the facts imposed by aging, mortality, and resignations. Our current figures show that there is an annual toll of the active membership due to combined causes amounting, in the case of a society with a membership around 600 and an average age at election of 35 years, of about 5 per cent. Thus 25 to 30 new members must be added each year to replace losses, and, if last year is a fair example, this means that 35 qualified biologists should be elected to our Society annually to permit the most modest growth. Over the past 20 years, the average number of new members elected annually was 26.5; but in 1948 and 1949 the number fell to 11 and 4, respectively. The retiring Secretary wishes to point out that very few such years would lead to the financial collapse of the Society. I urge the officers and members of the Society not to neglect this imperative obligation to nominate and elect worthy new members in sufficient number. Otherwise the Society had better frankly discontinue its policy of limiting membership to those whose continued scientific productivity and broad biological interests most merit the name of "naturalist."

This year 11 members of the Society sent in nominations to membership. The Secretary thanks them for their devotion to the interests of the Society and their considerable labor, and wishes there had been ten times as many,

so as to ensure a balanced growth of the Society. The Society elected 43 new members at the Ithaca meeting, and by November 1, 1952, acceptances had been received from 30. There are thus, at the present time, 480 active members, and a total of 650 members.

At the Annual Meeting it was voted to hold the next meeting in December, 1953, at Boston, with the American Association for the Advancement of Science. This departure from the practice of meeting in September with the A.I.B.S. was made because of the probable absence of many members of the Society during August and early September, 1953, on account of the international congresses of genetics and of zoology meeting at that time in Europe. It is not contemplated that the change to December will be permanent. The Society will also probably be represented on the A.I.B.S. program at Madison, Wisconsin, in September 1953, by cosponsorship of one or more symposia.

The Nominating Committee (M. R. Irwin, Chairman; Norman H. Giles, C. P. Oliver) presented the names of Louis J. Stadler, Professor of Field Crops, University of Missouri, and Principal Geneticist, U. S. Department of Agriculture, for the office of President of the Society; Alexander Hollaender, Director of the Biological Division of the Oak Ridge National Laboratory, for Vice-President; and Warren P. Spencer, Professor of Biology, Wooster College, for Secretary, 1953–1955. No further nominations being made, these officers were unanimously elected. H. H. Plough has been appointed by the President of the Society to serve as Society Representative on the AAAS Council, 1952–54.

The appointment of David D. Keck, New York Botanical Garden, to the editorial board of *The American Naturalist,* was confirmed by the Executive Committee.

The appropriation of $300.00 from the Society's treasury to take care of the costs of the editorial office of *The American Naturalist,* in lieu of a similar sum previously provided by the publisher, was approved by the Executive Committee and the Society. This solution to the problem of increasing costs of publication was preferred to any increase in the Society's dues at the present time.

A resolution of warm appreciation was passed unanimously to thank Dr. Sanford S. Atwood of Cornell University for his effective and untiring labor as our local representative in arranging the Annual Meeting; to thank our host institution, Cornell University, for its generous hospitality; and to thank Dr. Samuel L. Meyer, new Executive Director of the A.I.B.S., Dr. Clarence Hylander, and the other staff members of the AIBS, for their fine arrangements for a meeting that, by general consensus, was the best biological meeting yet held.

Respectfully submitted,
BENTLEY GLASS
Secretary

JOHNS HOPKINS UNIVERSITY
BALTIMORE 18, MD.
October 30, 1952

NEW MEMBERS, 1951

(Additional to those reported in January, 1952, issue of *The American Naturalist*)

Henry N. Andrews, Jr., Botanical Museum, Harvard University
Vernon I. Cheadle, University of Rhode Island
P. P. H. De Bruyn, University of Chicago
J. Wyatt Durham, University of California
E. Gorton Linsley, University of California
C. L. Newcombe, U. S. Public Health Service,
Oliver P. Pearson, University of California
Keith R. Porter, Rockefeller Institute for Medical Research
Kenneth B. Raper, University of Chicago
T. C. Scheirla, American Museum of Natural History
Nelson T. Spratt, University of Minnesota

NEW MEMBERS, 1952

K. C. Atwood, Oak Ridge National Laboratory
William K. Baker, Oak Ridge National Laboratory
Albert P. Blair, University of Tulsa
Guy Weston Bohn, U. S. Department of Agriculture, La Jolla
Vaughan T. Bowen, Brookhaven National Laboratory
W. R. Breneman, Indiana University
John Langdon Brooks, Yale University
Herman B. Chase, Brown University
Lamont C. Cole, Cornell University
Alan D. Conger, Oak Ridge National Laboratory
James F. Crow, University of Wisconsin
Howard J. Curtis, Brookhaven National Laboratory
A. Brito da Cunha, University of Sao Paulo, Brazil
Allen S. Fox, Ohio State University
D. L. Fox, Scripps Institute of Oceanography
D. U. Gerstel, North Carolina State College
Aubrey Gorbman, Barnard College, Columbia University
Sam Granick, Rockefeller Institute for Medical Research
Margaret C. Green, Ohio State University
D. S. Grosch, North Carolina State College
Caryl P. Haskins, Haskins Laboratories
Irwin H. Herskowitz, Indiana University
Franz J. Kallmann, New York State Psychiatric Institute
C. C. Li, University of Pittsburgh
Charles B. Metz, University of North Carolina
Frederick H. Osborn, American Eugenics Society, New York
Elizabeth Shull Russell, Roscoe B. Jackson Memorial Laboratory
Drew Schwartz, Oak Ridge National Laboratories
Emil L. Smith, University of Utah School of Medicine
Stanley G. Smith, Forest Insect Laboratories, Canada
Arthur G. Steinberg, Children's Hospital, Boston
Clyde Stormont, University of California (Davis)
Bruce Wallace, Long Island Biological Association, Cold Spring Harbor, N. Y.
Sherwood L. Washburn, University of Chicago
J. Walter Wilson, Brown University

DEATHS REPORTED SINCE LAST REPORT

Sherman C. Bishop
T. H. Bissonnette
J. C. Cartledge
M. C. Ferguson
Harold Kirby
W. M. Smallwood

SUMMARY OF TREASURER'S REPORT, 1952

The Treasurer's books were audited by E. W. Caspari and E. S. Deevey on January 2, 1952, and found to be correct. The balance at that time was $1346.83. Receipts for dues and subscriptions from January 2 to September 5 amounted to $2080.50. Expenditures for the same period were $1510.85, leaving a balance of $1916.48, out of which the annual contribution of the Society to the AIBS of approximately $225.00, the expenses of publishing the Secretary's records for the triennium, and the expenses in connection with the Ithaca meeting must be paid. The balance at the end of the year should thus be slightly higher than at the beginning.

D. F. POULSON,
Treasurer

YALE UNIVERSITY
NEW HAVEN, CONN.
October 30, 1952

ERRATA

In the article "An Analytical Study of the Geographic Distribution of *Rana septentrionalis*" in THE AMERICAN NATURALIST, Vol. LXXXVI, January-February, 1952, by John A. Moore, the caption for Figure 3 on page 8 should read: "Geographic distribution of *Rana catesbeiana, Rana septentrionalis,* and *Rana clamitans* in Michigan." This was incorrectly labelled Wisconsin.

ADVICE TO AUTHORS

THE AMERICAN NATURALIST will welcome articles which contribute to the purposes outlined on the inside front cover.

Material intended for publication should be prepared to conform to the style adopted in the issues beginning in January 1951. It should be typewritten with double spacing, leaving a two inch margin at the right for editorial directions. Each table should be typed on a separate sheet. Footnotes to text statements should be avoided since they can usually be included in the text, parenthetically if necessary. Where unavoidable, they should be numbered consecutively and typed on a separate sheet, since they will be set in a different type size. Footnotes to tables are often necessary; they should be designated by asterisks, daggers and similar signs to avoid confusion with the numerals in the tables.

Legends for figures should be typewritten on separate sheets. The illustrations are sent to the engraver, the legends to the printer.

Each article, except letters to the Editors, should contain a brief summary.

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